

THE JOURNAL OF THE
 AMERICAN SOCIETY OF
 ZOOLOGISTS
 VOLUME 12, NUMBER 2
 1993

CO-EDITORS

Lesley J. Rogers
Division of Neuroscience &
Animal Behaviour
University of New England
Armidale NSW 2351
AUSTRALIA

Sally A. McFadden
Dept. of Psychology
The University of Newcastle
NSW 2308
AUSTRALIA

EDITORIAL ADVISORY BOARD

Ruben Ardila
University of Colombia
Apartado 88754
Bogota Colombia S.A.

Juan D. Delius
Allgemeine Psychologie
Universitat Konstanz
D-78434 Konstanz 1
GERMANY

Jack Demarest
Department of Psychology
Monmouth University
West Long Branch
NJ 07764, USA

Gordon G. Gallup Jr
Department of Psychology
SUNY at Albany
Albany, NY 12222 USA

Gary Greenberg
Dept. of Psychology
Wichita State University
Wichita, Kansas
67260-0034 USA

R. Bryan Jones
Roslin Institute
(Edinburgh), Roslin
Midlothian EH25 9PS
SCOTLAND

Peter Klopfer
Department of Zoology
Duke University, Durham
NC 27706 USA

Mauricio R. Papini
Department of Psychology
Texas Christian University
Fort Worth, TX 76129 USA

Wojciech Pisula
Faculty of Psychology
University of Warsaw,
Stawki 5/7
00-183 Warsaw POLAND

Emanuela Prato Previde
Istituto di Psicologia della
Facolta Medica
Universita di Milano, via T.
Pini 1
20134 Milano, ITALY

Michael Renner
Department of Psychology
West Chester University,
West Chester
PA 19383 USA

Leickness C. Simbayi
Department of Psychology
University of Fort Hare
Private Bag X1314
Alice 5700, SOUTH
AFRICA

Roger K. Thomas
Department of Psychology
The University of Georgia,
Athens
GA 30602-3013, USA

Ethel Tobach
American Museum of
Natural History
Central Park West at 79th St
New York 10024-5192,
USA

Dora F. Ventura
Instituto de Psicologia
University of Sao Paulo,
Cx. Postal
Sao Paulo, BRAZIL

Jeannette P. Ward
Department of Psychology
The University of Memphis
Memphis, TN 38152 USA

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

Volume 12, Number 2, 1999

**Gender Differences in Marmosets and Tamarins:
Responses to Food Tasks**

*Hilary Box, Maria Emilia Yamamoto and
Fivia Araujo Lopes*

59

**Intra- and Inter-specific Social Learning of a Novel
Food Task in Two Species of Tamarin**

Mark J. Prescott and Hannah M. Buchanan-Smith

71

**Factors associated with exploration in marmosets:
Age, gender and hand preference**

L. J. Rogers

93

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY is sponsored by the International Society for Comparative Psychology, an affiliate of the International Union of Psychological Sciences. In consonance with the goals and activities of the Society, it publishes reports of studies in the evolution and development of behavior of all species; on the use of the comparative method for the understanding of behavioral processes; and the examination of the adequacy of psychological and evolutionary theories. It accepts articles that deal with historical and contemporary relationships between humans and other animals; that elucidate problems of ecological and behavioral processes in resource management; that explicate fundamental concepts about human evolution; and that present research results and develop theories about the development and evolution of behavior. Articles on the contemporary and historical organization of knowledge about comparative psychology; promoting public education on the evolution and development of behavior; and about the training of students in comparative psychology are also invited. Book reviews; letters discussing published articles with replies by authors; notices of new books, journals, meetings and competitions or other matters of interest to the readers will be published at the discretion of the editors. The Editors and Associate Editor are elected by the Operations Committee of the Society. The Editorial Advisory Board is appointed by the Editors and the Operations Committee.

MANUSCRIPTS should be submitted in triplicate to the Editors. See inside back cover for style requirements.

SUBSCRIPTION inquiries and subscription orders to institutions and individuals who are not Society members should be addressed to International Society for Comparative Psychology, P.O. Box 1897, Lawrence, KS 66044-8897, USA, Telephone 913-843-1221, or Fax 913-843-1274. Subscription inquiries and subscription orders for Society members should be addressed to Professor Robert M. Murphey, Secretary, International Society for Comparative Psychology, Department of Psychology, University of California, One Shields Ave., Davis, California 95616-8686 U.S.A.. Telephone: (530) 752-1855; Fax: (530) 752-2087.

Subscription rates:

Volume 12, 1999 (4 issues) \$95.00 (outside the U.S., \$110.00). Members of the International Society for Comparative Psychology receive their yearly subscription as part of their membership dues. For membership information see back pages.

INDEXED OR ABSTRACTED IN: Psychological Abstracts.

PHOTOCOPYING: Authorizations to photocopy items for internal and personal use of specified clients is granted by the International Society for Comparative Psychology for users registered with the Copyright Clearance Center (CCC) Transactional Reporting Service, provided that the flat fee of \$6.50 per copy per article (no additional per-page fees) is paid directly to CCC, 27 Congress St., Salem, MA 01970. For those organizations which have been granted a photocopy license by CCC, a separate system of payment has been arranged. The fee code for users of the Transactional Reporting Service is: 0889-3667/91/\$6.50.

COPYRIGHT 1999 by the International Society for Comparative Psychology. Published quarterly.

GENDER DIFFERENCES IN MARMOSETS AND TAMARINS: RESPONSES TO FOOD TASKS

Hilary Box
University of Reading, UK

Maria Emilia Yamamoto and Fivia Araujo Lopes
Universidade Federal do Rio Grande do Norte, Brazil

ABSTRACT: The study of behavioural gender differences among Callitrichid primates has been generally neglected. We describe evidence from experimental studies in which adult female tamarins (*Saguinus*) and marmosets (*Callithrix*) demonstrate priority of access to food that is spatially and temporarily restricted. Differences in behavioural strategies between both reproductive and non-reproductive females, and males, are consistent with differences between the genera in their feeding ecology and social organisation. They are also functionally plausible. A recent study gives preliminary data to show that, although mated females in family groups of common marmosets demonstrate priority of access to food sources, overall there are differences in responsiveness that may be influenced by factors such as the time of feeding, energy content and preference of food.

Gender differences among the primates in their feeding behaviour include examples in which adult females demonstrate a priority of access to food (eg Jolly, 1984; Richard, 1987). This is unusual among primates and raises a number of interesting theoretical questions. For example, considerations of functional hypotheses to account for such phenomena include reproductive exclusivity within a small number of adult males and females. The case is most easily explained in the context of monogamy, as in some lemurs and in which paternity is relatively certain. The argument is that male deference to a breeding or potentially breeding female will benefit the future survival of the offspring of that female (eg Richard, 1987).

Address correspondence to Hilary O. Box, Department of Psychology, The University of Reading, Reading RG6 6AL, UK.

The aim of the present paper is to discuss aspects of female priority of access to food among species of tamarins and marmosets. Moreover, in the majority of our experiments at Reading, we have used very simple food tasks in which different species could reach in and take pieces of fruit. These tasks are a kind of embedded food situation that is part of the natural feeding behaviour of these animals. Hence, we have made use of environmental challenges that provide controlled experimental conditions to probe natural behavioural propensities of responsiveness. They are useful for probing differences among species as well as specific behaviour within species.

One experiment in particular led to significant and interesting results, not least because it had a 'respectable' sample size (Box *et al.* 1995). We have presented a series of perspex food boxes (see Figure 1) that measured 15 x 6 x 10cm, with an ample supply of small pieces of chopped apple, into the home cages of 14 pairs of male and female tamarins (*Saguinus* spp.) for 20 min at a time. The idea was to construct simple tasks that varied in complexity and stimulated ongoing interest and activity in the monkeys.

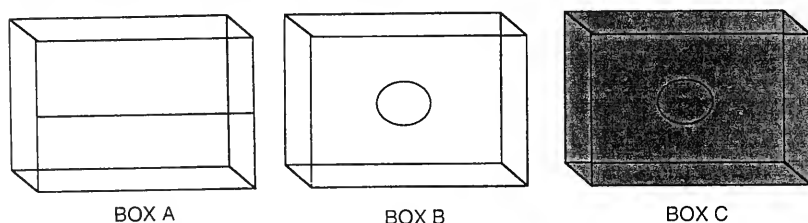


Figure 1. Plastic foraging boxes.

There were 5 pairs of male and female saddle backs (*Saguinus fuscicollis*), 5 pairs of male and female red bellied (*S. labiatus*) and 4 pairs of male and female cotton tops (*S. oedipus*). Baseline observations of activities were made before the experiment began, as well as before each presentation of a food task. These included frequencies and durations of huddling and proximity within the pairs, of feeding, drinking and locomotion in addition to frequencies of scent marking and aggressive behaviour. When the boxes were present, categories of behaviour also included directly approaching the tasks when looking at them, investigation (looking at and manipulating the boxes), attempts to remove food, and successes at removing the food from the boxes. The tasks were presented in a counterbalanced order, and all behaviour was recorded in real time with an on line computer system. The results were calculated using ANOVAS in which the main

variables were the species, the different boxes, and the gender of the tamarins.

It was interesting to note that the saddle backs showed a significantly different profile of responsiveness compared to other species. They were more 'cautious' in their behaviour, as shown by the fact that they approached the boxes less frequently and for less time than either of the other species. Interestingly, these observations contrast with observations of the species in nature, in response to food baited traps and at least in the context of associations with another species of tamarin (Box, pers observation cited Box, 1984; Buchanan-Smith, 1990). Species differences of these kinds are useful to help to build up a body of information that is relevant to the comparative behavioural ecology of the group, as well as towards their management in captivity. However, with reference to our experiment, it was the results on gender differences across all three species of tamarins that raised theoretically interesting questions. We found that the females attempted the tasks more often and for longer than the males, and with greater success in obtaining food. It was also important to find that all the animals were able to solve all the tasks. Again there were no significant differences between the males and females in the amount of time that they spent in investigating the tasks generally, and there were no obvious motivational differences in terms of their energy requirements. Males and females are of equivalent body size, and the females were not pregnant at the time. The crux of the matter was that the significant differences in behaviour between males and females related specifically to successful foraging from the food tasks.

It is also relevant to note here that additional evidence in this context was given in that we also found subsequently (Box and Rohrerhuber, unpublished data) that the same adult pairs of animals that were used in the present study showed no gender differences in behavioural responsiveness in daily trials in which they had limited daily access to large unfamiliar outside areas to which their home cages were tunnelled. In other words, responses to new spatial opportunities differed from those given to new foraging opportunities.

In the food task study we concluded that females showed priority of access to the food which, in that case, was a preferred food. Moreover, we found no evidence for overt competition between males and females in the food task situation. Females did not defend the preferred food. There was some increase in aggression within the pairs when the food tasks were present, but there was no aggressive behaviour in the areas around the food boxes. In fact, males often sat

near the females when they were feeding from the boxes and 'looked on'. We described the males as deferring to the females when they fed. There are some other, if few, experiments that concur with these results, and interestingly, within the context of tamarin family groups as in cotton tops (Tardif and Richter, 1981). These also show female priority of access in food 'tasks'.

From a functional perspective it is interesting to consider that deference to a breeding female is advantageous in the context of the communal rearing system of callitrichids that support the energetic demands of multiple births, postpartum oestrous and pregnancy, together with lactation. It is also advantageous in that there is a small number of potentially breeding partners. From a male perspective, we may consider behaviour that is consistent with the protection of his genetic investment including mate guarding and vigilance. From the female perspective, priority of access to preferred and restricted sources of food may be a critical strategy in terms of their energetic demands. Further, it is also the case that non-breeding females may show priority of access to food, as in our experiment with tamarins. Hence, it is also relevant to consider that, apart from the direct energetic influences of reproductive status, females may have different characteristic propensities in foraging situations than males. These differences may become accentuated with regard energetic demands, but females may behave differently from males *per se* in some feeding situations. Moreover, it has also been of interest to discuss differences in behavioural strategies among males and females of species of different genera, and to find that these are consistent with differences between them in terms of their social organisation and feeding ecology (Box, 1997) when supplemental food is presented in spatially and temporarily restricted conditions. In essence, marmosets have been found to defend food assertively (cf Box, 1997), and it is relevant in this context to consider the following (cf Box 1997).

First, that marmosets and not tamarins have specialised dentition for gauging holes in plant material to feed on exudates. Exudates are highly nutritious foods that frequently require energy to obtain. Moreover, and importantly, such food is defensible. Second, that marmosets have home ranges that are smaller than those of tamarin species, and their mating systems tend more towards monogamy. These factors are consistent with the behaviour of marmosets in which adult females obtain priority of access to important static sources of food, by competitive strategies, and the males are relatively secure in their reproductive fitness and inclusive fitness. Third and by contrast,

the natural co-operative nature of tamarin social interactions (Caine, 1993) is consistent with their larger home ranges and relatively unstable social units in which there are more adult males, and paternity is comparatively uncertain. Further, tamarins do eat plant exudates, but this feeding is opportunistic, and does not involve defensible food at particular sites; food is generally more widely scattered. We may consider then that the adult males of different genera may behave differently with regard to female priority of access to food. Male tamarins for instance, may show a greater diversity of functions with regard to feeding situations than do marmosets. These strategies may include mating opportunities. Possibilities will vary according to species and social context. From the perspective of breeding females of all species, however, priority of access may be a critical strategy in terms of their energetic demands. However, it is also clear that non breeding females of different genera may show priority of access to food. Hence, we should consider that, apart from the direct influence of reproductive status, males and females have different characteristic propensities of responsiveness in such as foraging situations. Overall, the results of our research showed robust findings which opened up a whole range of ideas for further study (see Box, 1997).

We have recently extended the work on gender differences in feeding strategies within our long standing collaboration among a number of Brazilian institutions and Reading University in the UK. We plan food task experiments with species of lion tamarins (*Leontopithecus spp*) supervised by Sr Alcides Pissinati at the Rio de Janeiro Primate Centre. Species of this genus have not been examined in the present context and pose some interesting questions (Box, 1997). Further, studies with common marmosets are in progress in captivity at the Universidade Federal do Rio Grande do Norte (UFRN) and at two field sites, namely, that of the UFRN at Nisia Floresta supervised by Dr Maria de Fatima Arruda and at that of the Universidade Federal Rural de Pernambuco (UFRPE) at Tapacura supervised by Dr Maria Adelia Monteiro de Cruz. For instance, because one aspect of central interest in considering gender differences among common marmosets is the relative assertiveness of adult females over desirable food that is restricted in time and space, it is of interest to consider this with reference to an energy model for priority to access to food in captivity. Hence, we consider the influence of reproductive status and assertiveness over food. The behaviour of adult males and females are observed at times of different reproductive energy expenditure. For example, given the energy demands of lactation, we may expect that

reproductive females will demonstrate more evidence of priority of access to food at these times – as by greater assertiveness in aggressive defensive behaviour. A series of preliminary studies has begun at the UFRN to test a number of such hypotheses. We indicate one such study here that raises a number of questions for future research.

METHOD

Subjects

Observations were made on 10 family groups. Five of these contained adult pairs that lived with between two and four offspring, and they produced infants during the observation period. The reproductive pairs of the other 5 similarly sized families did not produce offspring for some time during the course of the study. Importantly, and in contrast to studies mentioned earlier, these observations were made to food that was routinely given to the marmosets. This adds an additional dimension to measures of responsiveness in this domain. The use of novel foods and unfamiliar food tasks certainly require care that we do not confound responses in obtaining food, with differences between males and females in their responses to unfamiliar objects - as by exploration for example.

Procedure

In this study, each family was fed three different kinds of food each day, in the same order, and in a bowl that measured 13cm in diameter. The first meal of the day consisted only of fruit. The second morning meal was a mixture of fruit and cereals or fish fry. A third meal of bread, milk and vitamins was given later in the early afternoon. Each group of marmosets was observed 6 times a week with 2, 10 min observations for each type of meal. The method of sampling behaviour was by continuous recordings spoken into a tape recorder and subsequently transcribed on to data sheets. With reference to the current context, aggressive behaviour was recorded when individuals characteristically vocalised, cuffed, chased or bit another animal in the immediate vicinity of the food source. Note that all such behaviour occurs in short bouts and was, therefore, at this pilot stage, recorded as frequencies and not in durations. With regard to the reproductive status of the breeding females, the 'non-reproductive' families were observed

over a total of 4 consecutive weeks. Observations on families that produced infants during the study were made for 4 consecutive weeks after the births and for one (2 families) or two (3 families) weeks before it.

RESULTS

Figure 2 shows total mean weekly frequency scores of aggressive behaviour for the adult pairs together with those of their offspring of various ages. From these preliminary data and analyses by 2-way ANOVAS (age and reproductive status), the following points are worthy of emphasis. First, that the adult pairs of all the families were consistently more aggressive in the presence of food than other group members ($df = 3,69$ $F = 12.11$, $p = 0.0001$). Second, that within the adult pairs, the females were consistently more aggressive than males (LS means $p = 0.023$). Moreover, the females that gave birth during the study, were more aggressive than those that did not. Third, that these females were more aggressive over the food after a birth than before it. We may also note a non significant trend of increasing aggressiveness from non-reproductive females, to reproductive females before a birth, to reproductive females after a birth. It was also interesting to find that both males and females of the mated pairs (including those that did not reproduce around the period of the study) increased their aggressiveness in the presence of food compared with their offspring - that included a variety of ages. Hence, both parents may assert social status in the context of the food sources, with the females being more assertive with regard to their energy requirements (see also Box *et al.* 1995).

We have also noted (Lopes unpublished data) that the aggressiveness of the reproductive male in the presence of food was not addressed to his mate, but to his offspring. This raises questions as to whether the male aids his female in defence of food, for example, and more so at particular times of her reproductive cycle.

The results as depicted in Figure 2 fit the general expectations that we outlined earlier. It was also important, however, to look at the behaviour of the animals in the context of their different meals. Figure 3 shows relevant data. Hence, observations on the first meal of the day showed that all the mated females - both reproductive and non reproductive, were more aggressive over the food than any of the other animals (2 way ANOVA $df = 3,69$, $F = 12.74$, $p = 0.0001$). This meal has a special reference in two respects. First, it was the first meal after

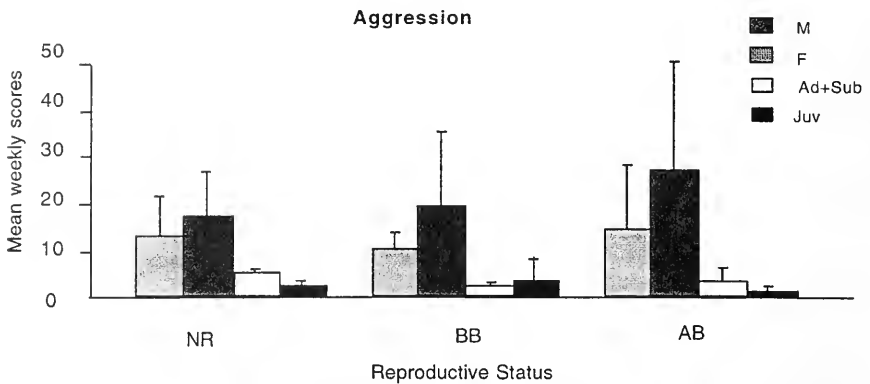


Figure 2. Total mean weekly frequency scores of aggressive behaviour for the adult pairs of marmosets that were non-reproductive (NR) and reproductive both before (BB) and after a birth (AB) together with the scores for the offspring of various ages.

a period without food, and second, it contained high energy food in the form of fruits. It was also of interest, however, to find that aggressive responsiveness to the foods was not consistent across the meals and times of day. Hence, reproductive females were more aggressive than non-reproductive females over food in the second meal, but there were no significant differences between either the non-reproductive and reproductive females, or between the reproductive females in the periods before and after a birth. In this condition, mated females overall were more aggressive in the presence of food than all other animals (2 way ANOVA $df = 3,69$ $F = 10.56$, $p = 0.0001$). Further, responses to the third meal were different from either of the first or second meals. In this case, the non-reproductive females were more aggressive than they were in the other meals. Again, and although it was not statistically significant, the mated males were more aggressive in these conditions than in either of the other meals.

Further, the aggressiveness of both the mated males and females did not differ significantly either between themselves or among the conditions of reproductive status, namely, non-reproductive, before a birth and after a birth ($df = 3,69$ $F = 6.67$, $p = 0.0006$ (LS means males and females, $p = 0.1842$). This pilot study then suggests some additional perspectives for captive studies. Hence, although in this case the meals were not presented in a counterbalanced order, the results do indicate the potential influence of temporal and nutritional factors. These will repay additional study and help to refine functional hypotheses of priority of access to food among these animals.

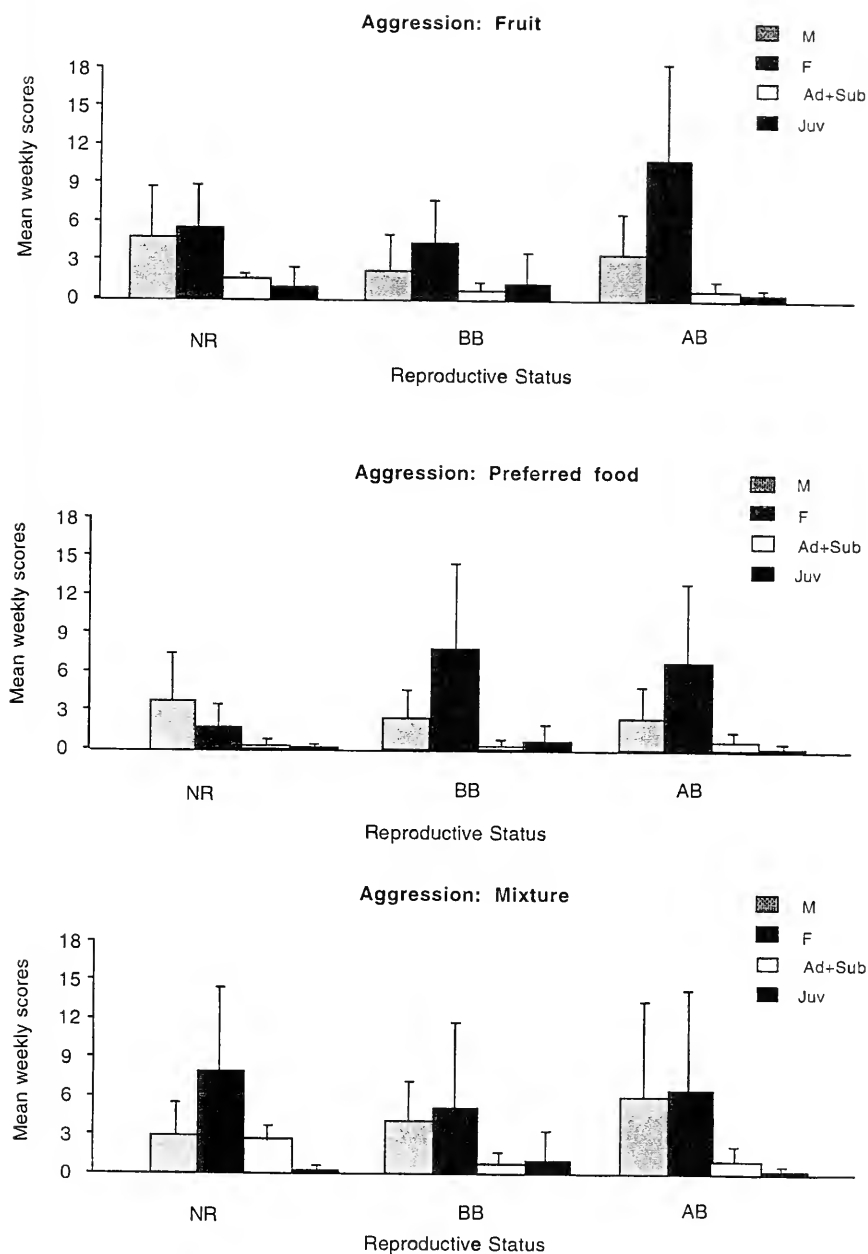


Figure 3. Total mean weekly frequency scores of aggressive behaviour for the adult pairs of marmosets that were non-reproductive (NR) and reproductive both before (BB) and after a birth (AB) together with the scores for the offspring of various ages – in the context of their different meals.

DISCUSSION

We wish to make two general points. First, to emphasise the value of environmental challenges as experimental techniques to provide controlled conditions to probe a range of comparative propensities of biobehavioural responsiveness among a wide diversity of animals. There are many good examples since the pioneering work of Alison Jolly in 1964, and Glickman and Sroges in 1966. The use of simple food tasks as described in the present, and related papers (Box *et al.* 1995; Box, 1997) provide additional cases.

The second general point is that compared with the vast majority of primate species discussions about behavioural differences between male and female callitrichids have been relatively neglected. Certainly, males and females look very similar and they behave similarly in many respects, and a lack of interest in this area is understandable. There are exceptions, of course, especially with reference to the behavioural and physiological control of reproduction in males and females (e.g. Abbott, 1991; Abbott and George, 1991; French and Inglett, 1991). There are also less systematic and small scale but nevertheless significant gender differences that deserve attention. For example, in captivity there is investigative behaviour of unfamiliar objects (Box, 1988) and spontaneous leaving of family groups (McGrew and McLuckie, 1986) and exploratory behaviour in an unfamiliar environment (Price, 1992) in all of which females have been found to be more responsive. In contrast, male tamarins have been observed to be less exploratory – initially at least, and more likely to be vigilant than females in unfamiliar environments (Price, 1991; Savage, 1990). A similar observation has been reported for common marmosets living in an unfamiliar area in captivity (Box, 1984) and by Koenig, (1998). See also Buchanan-Smith in this volume. There are also differences in vocal behaviour (Benz *et al.* 1980) and histological differences in scent glands that have implications for chemosignalling systems (Epple, 1994). Further, and again with potential reference to feeding, a proportion of all females of diurnal NWM species studied, are found to be trichromatic whereas males are consistently dichromatic (Jacobs, 1995). This suggests for example, that females may more easily discriminate and select among potential sources of foods than do males.

Recent work on female priority to food opens up additional perspectives. In all, we may consider that a neglect of behavioural gender differences in this group is a significant omission in our understanding of their biology. At this stage it is perhaps of particular

interest to emphasise gender differences between species of different genera. Once again, and as in previous studies, our present work with common marmosets is consistent with differences among marmosets (*Callithrix*) and tamarins (*Saguinus*) in their feeding ecology and social organisation.

ACKNOWLEDGEMENTS

We thank Lesley Rogers for her constructive comments on this manuscript.

REFERENCES

- Abbott, D.H. (1991) The social control of fertility. In: (Ed) H.O. Box, *Primate Responses to Environmental Change* (pp.75-89). Chapman and Hall.
- Abbott, D.H. & George, L.M. (1991) Reproductive consequences of changing social status in female common marmosets. In H.O. Box (Ed.), *Primate Responses to Environmental Change* (pp. pp.295-309). Chapman and Hall.
- Benz, J.J., French, J.A. & Leger, D.W. (1990) Sex differences in vocal structure in a Callitrichid primate *Leontopithecus rosalia*. *Am. J. Primatol.*, 21, 257-264.
- Box, H.O. (1984) *Primate Behaviour and Social Ecology*. Chapman and Hall.
- Box, H.O., Rohrhuber, B. & Smith, P. (1995) Female tamarins (*Saguinus* - *Callitrichidae*) feed more successfully than males in unfamiliar foraging tasks. *Behav. Processes*, 34, 3-12.
- Box, H.O. (1988) Behavioural responses to environmental change. Observations on captive marmosets and tamarins (*Callitrichidae*). *Anim. Technol.*, 39, 9-16.
- Box, H.O. (1997) Foraging Strategies among Male and Female Marmosets and Tamarins (*Callitrichidae*): New Perspectives in an Underexplored Area. In H.O. Box & H.M. Buchanan-Smith (Eds.), *Biology and Conservation of New World Primates*, *Folia Primatol.*, 68, 296-306.
- Buchanan-Smith, H.M. (1990) Polyspecific association of two tamarin species *Saguinus labiatus* and *Saguinus fuscicollis* in Bolivia. *Am. J. Primatol.*, 22, 205-214.
- Caine, N.G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organisation and behaviour. The role of predation pressures. In A.B. Rylands (Ed.), *Marmosets and Tamarins: systematics Behaviour and Ecology* (pp.200-219). OUP.
- Epplé, G. (1994) Gender differences in chemosignalling systems of Callitrichid monkeys: A review. *Abstr. 15th Congress Int. Primatol. Soc. Bali*, p.330.
- Ferrari, S. & Lopes Ferrari, M.A. (1989) A re-evaluation of the social organisation of the *Callitrichidae* with reference to the ecological differences between genera. *Folia Primatol.*, 52, 132-147.
- French, J.A. & Inglett, B.H. (1991) Responses to novel social stimuli in Callitrichid monkeys: A comparative perspective. In H.O. Box (Ed.), *Primate Responses to Environmental Change* (pp.274-294). Chapman and Hall.
- Glickman, S.E. & Sroges, R.W. (1966) Curiosity in zoo animals. *Behaviour*, 26, 151-

188.

- Jacobs, G.H. (1995) Variations in primate colour vision: Mechanisms and utility. *Evol. Anthropol.*, 3, 196-205.
- Jolly, A. (1964) Prosimians manipulation of simple object problems. *Anim. Behav.*, 12, 560-70.
- Jolly, A. (1984) The puzzle of female feeding priority. In M.F. Small (Ed.) *Female Primates: Studies by Women Primatologists* (pp.197-215). NY Liss.
- Koenig, A. (1998) Visual scanning by common marmosets (*Callithrix jacchus*): Functional aspects and the special role of adult males. *Primates*, 39, 85-90.
- McGrew, W.C. & McLuckie, E.C. (1986) Philopatry and dispersion in the cotton-top tamarin (*Saguinus (O) oedipus*): An attempted laboratory simulation. *Int. J. Primatol.*, 7, 399-420.
- Price, E.C., McGivern, A.M. & Ashmore, L. (1991) Vigilance in a group of free-ranging cotton-top tamarins (*Saguinus oedipus*). *Dodo J Jersey Wildl. Preserv. Trust*, 27, 41-49.
- Price, E.C. (1992) Adaptation of captive-bred cotton-top tamarins (*Saguinus oedipus*) in Colombia. PhD thesis University of Wisconsin, Madison.
- Richard, A.F. (1987) Malagasy prosimians: Female dominance. In B.B. Smuts, R.M. Cheney, R.W. Seyfarth, R.W. Wrangham, T.T. Struhsaker (Eds.), *Primate Societies* (pp.25-33). University of Chicago Press.
- Tardif, S.D. & Richter, C.B. (1981) Competition for a desired food in family groups of the common marmoset (*Callithrix jacchus*) and the cotton top tamarin (*Saguinus oedipus*). *Lab. Anim. Sci.*, 31, 52-55.

INTRA- AND INTER-SPECIFIC SOCIAL LEARNING OF A NOVEL FOOD TASK IN TWO SPECIES OF TAMARIN

Mark J. Prescott and Hannah M. Buchanan-Smith
University of Stirling, Scotland UK

ABSTRACT: Intra- and inter-specific social learning was investigated in two species of New World monkey, the saddle-backed tamarin (*Saguinus fuscicollis*) and the red-bellied tamarin (*S. labiatus*), which form stable and permanent mixed-species troops in the wild. We explored whether improved food acquisition, through social learning, is a potential advantage of mixed-species troop formation by allowing a pair of naive observers to watch a pair of trained demonstrators complete a novel foraging task. The aims of the study were (a) to determine if individuals succeeded at the task more quickly after having observed demonstrators, (b) to investigate whether speed of acquisition differed after observation of conspecific demonstrators as opposed to congeneric demonstrators, and (c) to compare performance between species. The number of trials taken by observers to succeed on the task was compared with that taken by naive demonstrators to succeed on the task initially. Individuals succeeded on the task more quickly if they had had the opportunity to watch demonstrators perform the task, regardless of whether the demonstrator was a conspecific or congeneric. There was no difference in performance between species. It is concluded that, for both species, the learning of a new foraging technique is facilitated by the presence of both conspecifics and congenics and that the likely mechanism for this facilitation is a combination of stimulus enhancement and response facilitation. Social learning of this kind is discussed with respect its adaptive value in wild mixed-species tamarin troops.

Tamarins of the genus *Saguinus* are small bodied (300-550g: Hershkovitz, 1977), diurnal, arboreal, South American primates which feed primarily upon insects, ripe fruits, nectar, and plant exudates (Snowdon and Soini, 1988; Garber, 1993). Their social lives are characterised by high levels of co-operation, tolerance and adaptability (Caine, 1993). When travelling and foraging troop members move in a cohesive manner (e.g., Yoneda, 1984a; Goldizen, 1987 for *S. fuscicollis*; Garber, 1988a for *S. mystax*; Buchanan-Smith, 1989 for *S.*

Address correspondence to Mark J. Prescott, Scottish Primate Research Group, Department of Psychology, University of Stirling, Stirling, FK9 4LA Scotland U.K.

labiatus) and when palatable food is found, food calls are given which are thought to recruit troop mates to the vicinity of the caller (Caine *et al.*, 1995 for *S. labiatus*). Tamarins also produce contact calls (Moody and Menzel, 1976 for *S. fuscicollis*; Caine and Stevens, 1990 for *S. labiatus*) which allow individuals to keep track of their troop mates, thereby maintaining cohesiveness within the troop, enabling movement in a co-ordinated manner and permitting co-operative ventures such as infant care and vigilance (Caine and Stevens, 1990). Furthermore, intra-troop aggression is rare (Goldizen, 1989; Buchanan-Smith, 1990 for *S. fuscicollis*; Coates and Poole, 1983 for *S. labiatus*) and, in comparison with squirrel monkeys (*Saimiri*), tamarins are reported to be tolerant of each other's presence at a newly discovered food source (Mayer *et al.*, 1992 for *S. labiatus*).

Not only do tamarins co-operate intra-specifically, but also inter-specifically. *S. fuscicollis* forms stable and permanent mixed-species troops with three other species with which it is sympatric. These are *S. mystax* (Castro and Soini, 1977; Garber, 1988a,b; Heymann, 1990; Norconk, 1990; Peres, 1991, 1992a,b, 1993), *S. labiatus* (Yoneda, 1981; Pook & Pook, 1982; Buchanan-Smith, 1990; Hardie, 1998), and *S. imperator* (Terborgh, 1983). The most stable association is that between *S. fuscicollis* and *S. mystax*, that between *S. fuscicollis* and *S. labiatus* is intermediate, and *S. fuscicollis* and *S. imperator* associate the least (Heymann, 1997; Buchanan-Smith, in press). Associating species defend a shared home range in parallel against neighbouring mixed-species troops (e.g., Terborgh, 1983; Yoneda, 1984a; Garber, 1988b; Buchanan-Smith, 1990; Peres, 1991, 1992a) (each species directing its aggression towards its conspecific rival: Pook and Pook, 1982; Buchanan-Smith, 1990, 1991; Peres, 1992b) and co-ordinate their activity and movement to a remarkable degree, moving about the home range as a single cohesive unit (typically within 20-50m of each other: Buchanan-Smith, 1990; Heymann, 1990). Both species use vocal communication to maintain this intratroop cohesion (Castro and Soini, 1977; Pook and Pook, 1982; Norconk, 1990) and are known respond to each other's alarm calls (Buchanan-Smith, 1990 for *S. fuscicollis* and *S. labiatus*; Heymann, 1987; Peres, 1993 for *S. fuscicollis* and *S. mystax*; Terborgh, 1983; Windfelder, 1997 for *S. fuscicollis* and *S. imperator*). Participating species also exhibit high overlap in the percentage of plant species eaten (Terborgh, 1983; Garber, 1988a; Ramirez, 1989; Hardie, 1998). When feeding together at monopolisable food resources, however, the smaller *S. fuscicollis* is often either supplanted by its larger, dominant congeners (Terborgh, 1983; Heymann, 1990; Peres,

1991) or is forced to wait until its congeners have finished eating before it can gain access to the resource (Hardie, 1998).

Given such high levels of co-operation and cohesion within and between tamarin species, together with a tolerant nature towards others with food (at least intra-specifically), one might expect that social learning could play an important role in how these monkeys respond to food related challenges in both single- and mixed-species troops. It is generally accepted that there is a greater likelihood of social learning in tolerant species/societies exhibiting high levels of behavioural co-ordination (Cambefort, 1981; Coussi-Korbel and Frigaszy, 1995). For example, Weigl and Hanson (1980) suggest that the intra-specific tolerance shown by red-squirrels (*Tamiasciurus hudsonicus*) in deciduous areas may be especially conducive to observational learning and the efficient exploitation of diverse seasonal food resources.

We wished to investigate whether improved food acquisition, through social learning, could constitute a potential advantage of mixed-species troop formation. Although individual tamarins in mixed-species troops may accrue foraging benefits in a number of ways (for example, through increased insect capture rates: Klein and Klein, 1973; Pook and Pook, 1982; Peres, 1992a; or avoidance of previously used areas: Terborgh, 1983; Buchanan-Smith, 1990; Peres, 1992b), it is the hypothesis that species in mixed-species troops can increase their foraging efficiency by sharing or parasitising information regarding the location and nature of local food resources (Pook and Pook, 1982; Terborgh, 1983; Hardie, 1995; Peres, 1996) that lends itself most to tests in captivity. Tests with captive mixed-species troops of tamarins have proved useful in elucidating the costs and benefits of association. Hardie (1995) was able to show that *S. labiatus* is facilitated to approach objects placed low down in an enclosure after having observed *S. fuscicollis* approaching them. He suggests that *S. labiatus* may benefit in mixed-species troops from the increased responsiveness of *S. fuscicollis* in the lower part of their environment by allowing *S. fuscicollis* to expose itself to any potential danger first and/or by displacing it should the novel object prove beneficial.

The majority of laboratory studies of social learning phenomena have concentrated upon underlying mechanisms. Relatively few have focused on social influences on the transmission of learned behaviours in ways that inform us about the contributions of social learning to group-living animals (Laland *et al.*, 1993; Adams-Curtis and Frigaszy, 1995; Coussi-Korbel and Frigaszy, 1995). Moreover, with the exception of some ornithological studies, such as those by Krebs (1973)

and Rubenstein *et al.* (1977), the majority of studies of social learning have examined learning within species. Here we present data on social learning of a novel food task both within and between-species.

METHOD

Study Animals

The study animals were taken from nine troops of *S. fuscicollis* weddelli and nine troops of *S. labiatus labiatus* housed in separate, adjacent, standard captive indoor/outdoor (2 x 1.75 x 1.5 m / 1.95 x 1.55 x 3.5 m) enclosures, off-exhibit from the public, at Belfast Zoological Gardens, N. Ireland, U.K. The monkeys were allowed free access between the indoor and outdoor areas, except when experimental protocol dictated otherwise. Indoor and outdoor areas were well furnished with a network of dead branches. In addition, the outdoor areas supported live shrubbery. The monkeys were fed once daily a mixed-diet of fresh-fruit and vegetables and primate pellets. Their diet also contained a protein element of either marmoset jelly, chicken, eggs or occasionally insects. Freshwater was provided daily. The monkeys' ages were similar across species and ranged from 1 year to 13 years at the time of testing. The mean age for *S. fuscicollis* was 4 years 7 months and for *S. labiatus* was 4 years 5 months. All individuals were captive-born.

The Foraging Task

The tamarins were required to learn how to obtain pieces of banana, a highly preferred food, suspended from the roofs of their enclosures by lengths of string. This task was considered to be a novel one for the tamarins, in that they had not previously been presented with food in this way and had no previous experience with this type of apparatus, but it is related to the foraging behaviour of the species in the wild. In their natural habitat, *Saguinus* take mainly small-sized or pod-like fruit resources which are situated on the terminal branches of the periphery of the tree crown (e.g., *Inga* spp., *Brosimum* spp., *Pourouma* spp.) or else hang down from moderate-sized branches (e.g., *Cecropia* spp.) (Garber, 1986, 1987, 1988a,b; Hardie, 1998 for *S. fuscicollis*; Yoneda, 1981, 1984b; Hardie, 1998 for *S. labiatus*). These terminal branches are not sturdy enough to support an upright stance

(indeed, their thinness probably prohibits larger primate competitors from utilising these resources), so to reach the fruit the tamarins adopt a 'grasping' strategy whereby they hang upside down, suspended from the thin branches of the tree, usually by their legs only, but occasionally also using one of their arms, leaving the hands and mouth free for manipulation of the fruit (Hardie, 1998; Prescott, pers. obs.).

The behavioural components required to reach the food item in the experimental task were very similar to this grasping strategy. In order to obtain the food item, the monkeys had to climb up one of the enclosure sides to the roof, locomote by quadrupedal suspension across it, and upon reaching the string, pull it up with their hands whilst hanging bipedally (the length of the strings being longer than the length of an extended monkey hanging by his/her legs). These behavioural components were not assumed to be novel for the tamarins (bipedal hanging, lifting and pulling being part of the behavioural repertoire of all the study animals) but the specific sequence of these necessary to succeed on the task (in its totality) was.

Experimental Design

The basic experimental design followed that of Thorndike (1898) in which a demonstrator animal performs a task in front of an observer, the test then being whether the observer achieves some criterion of success on the task more quickly than when compared with a naïve animal who has not been allowed to observe a demonstrator.

The experiment was designed so that both species acted as demonstrators for their conspecifics and for their congeners, so that comparisons could be made both intra- and inter-specifically between demonstrators and observers. The experiment was designed in this way because it may be that one or both species learn from their congeners more quickly than they do from their own species, indicating an additional advantage of forming mixed-species troops over and above that due simply to an increase in troop size.

Such an experimental design also allows comparisons to be made between species in their rates of asocial learning (independent acquisition). If one of the demonstrator species, say *S. fuscicollis*, learns the task solution asocially more quickly than the other, then *S. labiatus* might benefit more from watching *S. fuscicollis* than they would from observing their conspecifics. This too would constitute an additional advantage to forming mixed-species troops for *S. labiatus*.

For the intra-specific condition, three male-female pairs of *S.*

fuscicollis performed as demonstrators for three male-female pairs of *S. fuscicollis*; and three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. labiatus*. Intra-specific demonstrator and observer pairs were always related (usually parents and offspring) because it is not advisable to house unfamiliar, unrelated individuals of the same species next to each other. Due to the territoriality of tamarins, they may fight viciously (Prescott, pers. obs.). The pairs were normally maintained as family troops and separated only for testing. To avoid confounding effects of age, the number of pairs of parents or offspring acting as demonstrators and observers was counterbalanced.

For the inter-specific condition, three male-female pairs of *S. fuscicollis* performed as demonstrators for three male-female pairs of *S. labiatus*; and three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. fuscicollis*. Interspecific demonstrator and observer pairs were normally maintained as mixed-species troops (and were therefore familiar with each other) and separated only for testing.

Testing was carried out between July and September, 1996, and between April and June, 1997. Species were tested in male-female pairs to minimise the stress of separation and to more closely resemble the social foraging environment of the wild. However, this meant that, in both the intra- and inter-specific conditions, the second monkey of each male-female pair to complete the task had had the opportunity to observe its pair-mate. Consequently, only the data for the first monkey of each pair to complete the task are used in the analysis. This means, also, that the data are not confounded by the possible presence of individuals who simply exploit the skills of others (in this case, steal the food from the successful individual) without learning those skills themselves, and as such block social learning and transmission (Giraldeau and Lefebvre, 1987; Frigaszy and Visalberghi, 1990; Beauchamp and Kacelnik, 1991).

Procedure

All tests were conducted before the tamarins' daily feed, to ensure they were motivated to obtain the food reward. The experimental procedure was as follows:

1. Two strings (50 cm in length) were suspended from the centre of the wire mesh roof of the outdoor portion of the enclosure of the male-

female pair to be tested, and each loaded with a piece of banana (2 cm in width), while the monkeys housed in all other cages were shut inside the indoor portions of their enclosures. The pair acting as demonstrators were then allowed to exit the indoor portion of their enclosure, after which the connecting door between the indoor and outdoor portions of the enclosure was closed. Recording started the moment the door was opened and continued for 30 minutes, or until both food items had been eaten, after which the strings were removed.

The pairs were presented with the task in this way, once per day, until both individuals had succeeded in obtaining the food at least twice. These animals were then considered to be 'trained demonstrators'. Data documenting their asocial learning of the task were termed 'naïve demonstrator data' and were later compared to that of observers.

2. Subsequent, daily trials involved shutting out the second pair (those in the role of observer), into the outdoor portion of an adjacent enclosure and allowing them to observe, through the mesh enclosure sides, the demonstrator-pair complete the task in a further three 30 minute trials. In each case, at least one of the demonstrators completed the task in each of the three trials.

3. Immediately following the third observed successful trial, the observers were presented with the task themselves in the outdoor portion of their own enclosure, with the adjacently housed demonstrators (and all other troops) shut indoors (to prevent 'interference' effects: see Zajonc, 1985; Zentall and Galef, 1988).

Recording Methods

Data were recorded directly onto a hand-held computer using THE OBSERVER 3.0 event recording program (Noldus, 1993). The time at which each individual approached within 15 cm of the string, touched the string, and obtained the food item were recorded.

Data Analysis

From the data collected, the latencies (in seconds) from exiting the indoor portion of the home enclosure to approach within 15 cm of the string, touch the string, and to obtain the food item, were determined for each individual in each trial. The latency for the first individual of

each pair to obtain the food item on its first successful trial was added to the number of preceding unsuccessful 30 minute trials for that individual. This corrected, 'true', latency was used for analysis. Statistical comparisons between role (naïve demonstrator or observer), species, or condition (intra-specific or inter-specific) were made using non-parametric Mann-Whitney U-tests (with significance set at $\alpha < 0.05$) because of sample-size limitations and deviations from normality.

RESULTS

Overall (pooling both species intra- and inter-specifically) observers, which had had the opportunity to observe completion of the task by trained demonstrators of either species, successfully obtained the food item significantly faster than those that had not observed (the naïve demonstrators) ($z = -3.32, p < 0.01$; Figure 1).

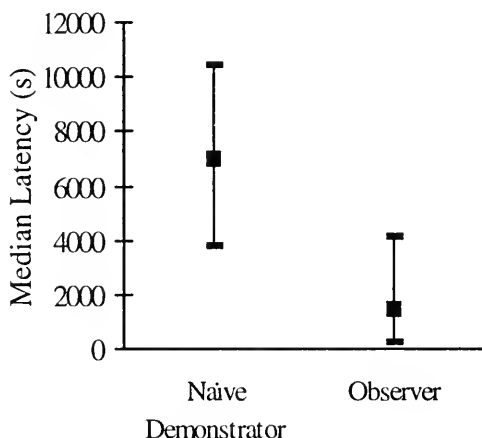


Figure 1. Median latencies (with interquartile ranges) to obtain food item for naïve demonstrators and observers, pooling species intra- and inter-specifically.

Collapsing across species, but splitting the data according to intra- and inter-specific conditions, it is found that, for both the intra- and inter-specific conditions, observers were significantly faster to obtain the food item than were their respective naïve conspecific and congeneric demonstrators ($z = -2.31, p < 0.05$, and $z = -2.02, p < 0.05$; Figure 2).

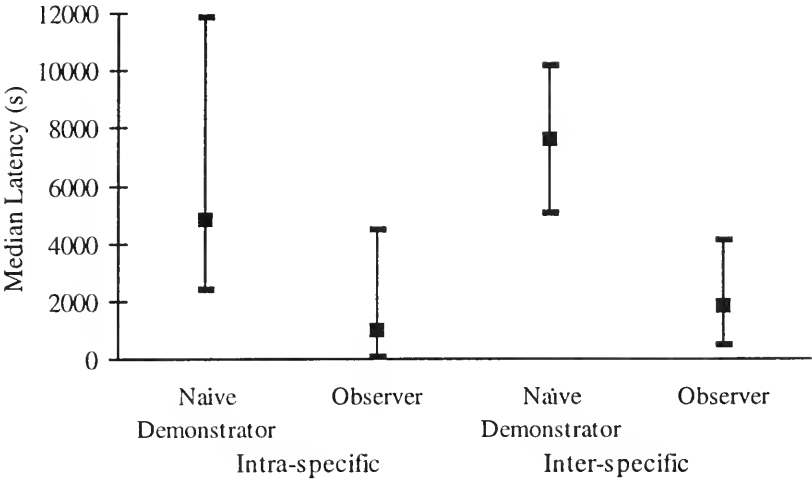


Figure 2. Median latencies (with interquartile ranges) to obtain food item for intra-specific and inter-specific naive demonstrators and observers.

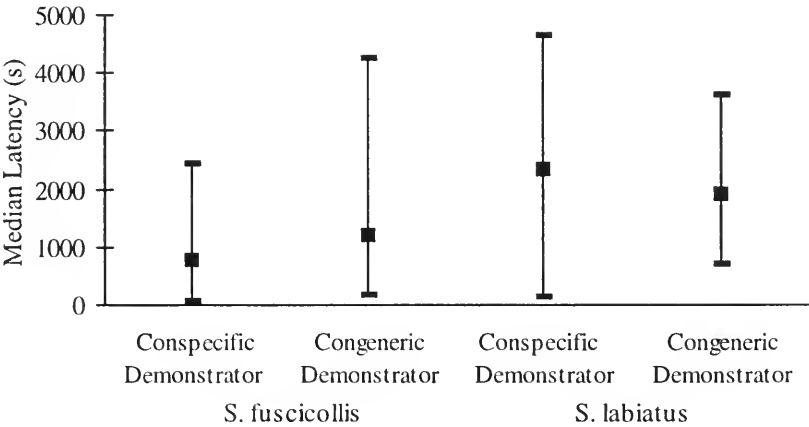


Figure 3. Median latencies (with interquartile ranges) to obtain food item for observer *S. fuscicollis* and *S. labiatus* after having observed conspecific or congeneric demonstrators.

No significant effect for demonstrator species was found. That is, for both *S. fuscicollis* ($z = -0.96, p > 0.05$) and *S. labiatus* ($z = 0.00, p > 0.05$), the latencies to obtain the food item after observing conspecific demonstrators did not differ from those after observing congeneric demonstrators. Nor was there a significant difference between the

latency to obtain the food item by observer *S. fuscicollis* after having observed *S. labiatus* demonstrators and observer *S. labiatus* after having observed *S. fuscicollis* demonstrators ($z = -0.40$, $p > 0.05$; Figure 3).

There was no significant difference between species in the rate of asocial learning by naïve demonstrators ($z = -0.12$, $p > 0.05$). Collapsing intra- and inter-specific conditions, there was no significant difference between species in the rate of social learning by observers ($z = -0.06$, $p > 0.05$; Figure 4). So, in addition to the absence of an effect for demonstrator species, species did not differ in their rates of learning either as naïve demonstrators or observers.

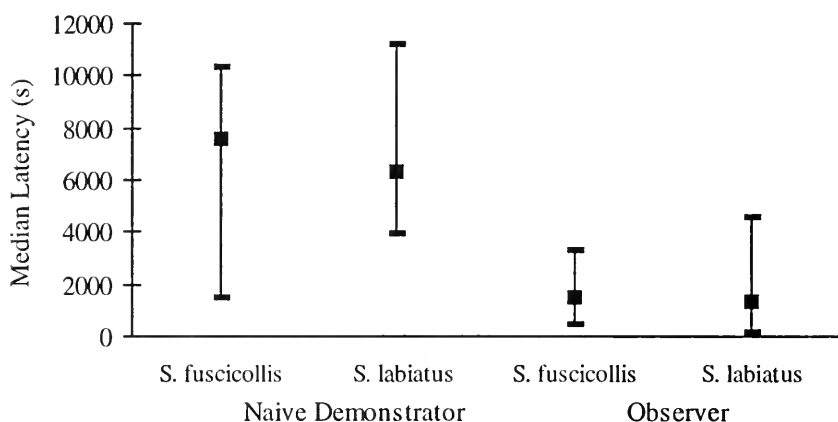


Figure 4. Median latencies (with interquartile ranges) to obtain food item for naïve demonstrator and observer *S. fuscicollis* and *S. labiatus*.

In order to reach a deeper understanding of what aspects of the demonstrator's performance may have influenced the acquisition of the technique necessary to reach the food item, a more detailed analysis of the behaviour and interactions during the acquisition period is needed. By examining the relations between the latencies to approach and touch the string, and to obtain the food item, we can identify exactly which of these behavioural components is facilitated by observation of a demonstrator. For example, it may be that the tamarins are facilitated merely to approach and touch the apparatus, and hence learn simply that it is non-threatening, rather than learning how to complete the task once in proximity to the apparatus. Indeed, the latencies to approach

Table 1. Median latencies (seconds) to approach within 15 cm of apparatus. P-values refer to Mann-Whitney U-test. Bold indicates a significant result.

Variable 1	Variable 2		Z value
	Naive Demonstrators	Observers	
Pooling species intra- and inter-specifically	4507	767	$z = -3.16, p < 0.01$
Intra-specific condition	3844	945	$z = -2.20, p < 0.05$
Inter-specific condition	5570	567	$z = -2.19, p < 0.05$
	Conspecific demonstrators	Congeneric demonstrators	
<i>S. fuscicollis</i> observers	747	1301	$z = -0.48, p > 0.05$
<i>S. labiatus</i> observers	945	251	$z = -0.64, p > 0.05$
	<i>S. fuscicollis</i>	<i>S. labiatus</i>	
Naive demonstrators	5145	4488	$z = -0.23, p > 0.05$
Observers	915	573	$z = -0.20, p > 0.05$
Observers from congeneric demonstrators	1301	251	$z = -0.58, p > 0.05$

Table 2. Median latencies (seconds) to touch the apparatus. P-values refer to Mann-Whitney U-test. Bold indicates a significant result.

Variable 1	Variable 2		Z value
	Naive Demonstrators	Observers	
Pooling species intra- and inter-specifically	5368	769	$z = -3.26, p < 0.01$
Intra-specific condition	4641	978	$z = -2.24, p < 0.05$
Inter-specific condition	6009	623	$z = -1.96, p > 0.05$
	Conspecific demonstrators	Congeneric demonstrators	
<i>S. fuscicollis</i> observers	752	1303	$z = -0.16, p > 0.05$
<i>S. labiatus</i> observers	1021	361	$z = -0.16, p > 0.05$
	<i>S. fuscicollis</i>	<i>S. labiatus</i>	
Naive demonstrators	6026	4794	$z = -0.17, p > 0.05$
Observers	917	684	$z = -0.29, p > 0.05$
Observers from congeneric demonstrators	1303	361	$z = -0.40, p > 0.05$

within 15 cm of the apparatus (Table 1) and to touch the apparatus (Table 2) all followed a similar pattern to the latencies to obtain the food item, with the exception of an absence of a significant difference in the latency to touch the apparatus for inter-specific naïve demonstrators and observers (Table 2). To examine whether the tamarins actually learnt how to complete the task, the following inter-behaviour latencies were calculated: (a) the latency to approach within 15 cm of the apparatus was subtracted from that taken to touch the apparatus to give the approach-touch latency; (b) the latency to approach the apparatus was subtracted from the latency to obtain the food item to give the approach-obtain latency; and (c) the latency to touch the apparatus was subtracted from the latency to obtain the food item to give the touch-obtain latency.

It was found that, overall (pooling both species intra- and inter-specifically) observers were facilitated to obtain the food item once within proximity to the apparatus ($z = -2.26, p < 0.05$) and once having touched the apparatus ($z = -2.33, p < 0.05$). Latency to touch the apparatus once within proximity to it was not facilitated by observation ($z = -1.74, p > 0.05$; Figure 5).

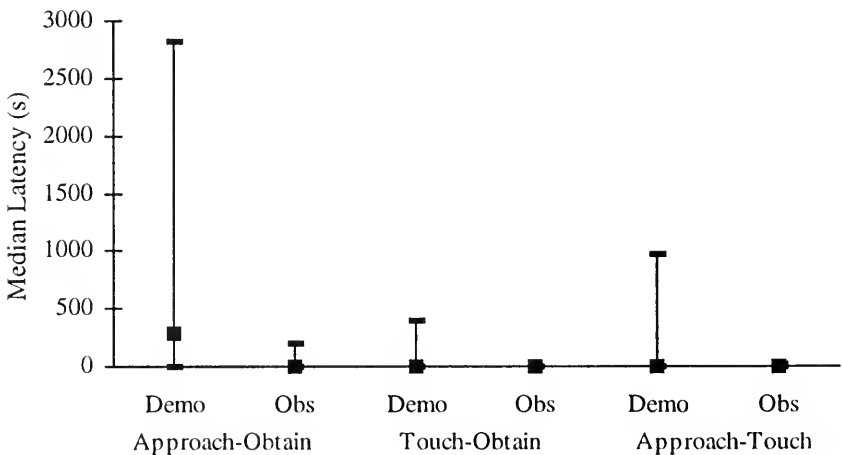


Figure 5. Median inter-behaviour latencies (between approach to obtain, touch to obtain and approach to touch) (with interquartile ranges) for naïve demonstrators (demo) and observers (Obs), pooling intra- and inter-specifically.

DISCUSSION

The aim of this study was to investigate whether observation of an experienced conspecific or congener has any influence on the rate at which an individual tamarin learns how to access food in a novel food task. The opportunity to observe an experienced individual clearly did lead to faster successful completion of the task than did asocial learning. Such a facilitatory effect may have considerable adaptive value in wild tamarin troops, in that individuals can benefit by learning about their changing environment more quickly, through observation of experienced troop members, than by asocial learning alone. *Saguinus* inhabit tropical rain-forests. These are generally characterised by high species diversity but low species density (Milton, 1988) and thus it is probable that foraging individuals will come across potentially exploitable but novel food resources. In addition, each new generation is likely to come into contact with foods not previously encountered. If learning how to exploit these resources can be facilitated by observation, then social learning will be an adaptive strategy in enabling the rapid, effective and safe exploitation of the novel food resources, possibly at reduced energy cost and predation risk. Rapid exploitation of fruit resources requiring the grasping strategy may be important for *Saguinus* as they are especially vulnerable on the thin, terminal branches of tree crowns, particularly to their main predators, raptors (Peres, 1993). Provided species can learn from each other, association, through an increase in troop size, would increase the opportunity for information transfer between individuals accordingly. Social learning of this kind may be particularly important for the younger members of the troop who, in their naive immaturity, face a host of new environmental challenges for which the need to rapidly acquire the behavioural solutions necessary for survival may be particularly acute (Galef, 1976).

With regards to the adaptivity of mixed-species troops per se, neither species showed a significant difference in their latency to complete the task after having observed a conspecific demonstrator as opposed to a congeneric demonstrator. This is perhaps surprising given that, in all mixed-species troops studied to date, inter-specific social interactions are rare in comparison to intra-specific ones (Pook and Pook, 1982 for *S. fuscicollis* and *S. labiatus*; Norconk, 1986; Heymann, 1990 for *S. fuscicollis* and *S. mystax*). Those inter-specific interactions that do occur are most often agonistic and associated with the exploitation of monopolisable plant food resources. This lack of an effect for demonstrator species may simply be an indication of the

considerable cohesion, integration and tolerance of tamarin mixed-species troops in the wild and in captivity. It is reported that more affiliative inter-specific interactions occur in captivity (e.g., grooming and social play: Heymann and Sicchar-Valdez, 1988; Heymann *et al.*, 1996; Hardie, 1997). Certainly both species of observer in this study spent brief but frequent periods of time intently observing their demonstrators behaviour at the apparatus, regardless of their species. Being able to learn from congeners as well as conspecifics may lead to an additional advantage to mixed-species troops over single-species troops, in that individuals can benefit from an increased knowledge base (i.e., the species-specific experience of their own species and that of their congeners). This possibility is important for tamarins given that, in all mixed-species troops studied thus far, there is vertical stratification between the associating species (with *S. fuscicollis* occupying a lower height than their congeners: Yoneda, 1981; Pook and Pook, 1982; Terborgh, 1983; Norconk, 1986; Buchanan-Smith, 1990) and thus the potential for differential knowledge regarding separate forest strata.

In this experiment, in addition to the absence of an effect for demonstrator species, there were no differences between species in their rates of learning, either as naive demonstrators or observers. Thus it cannot be concluded that mixed-species troops confer any additional advantage above that which would be accrued in monospecific troops of the same size. In any case, in the wild, large monospecific troops may be unattainable due to feeding competition and intra-sexual conflict between reproductive competitors (Buchanan-Smith and Hardie, 1997). Moreover, since there were no differences between the species in their rates of learning, and since *S. labiatus* having observed *S. fuscicollis* were no faster to complete the task than were *S. fuscicollis* after observing *S. labiatus*, the advantage accrued to each species from observing appears symmetrical.

Although we wished to concentrate upon the adaptive function of the monkeys' learning, in the context of mixed-species association, rather than the means by which it was achieved, we can speculate upon the mechanism at work. Identification of a mechanism is important in order to further our understanding of comparative primate intelligence. We are faced with the difficult task of sorting out a variety of processes occurring in social situations which can influence an observer's behaviour and lead to similar behaviours in the observer and observed. Our problem is thus one of exclusion of alternative mechanisms, an especially difficult problem given that there is no uniformly accepted classification of social learning mechanisms at present (e.g., Galef,

1988; Whiten and Ham, 1992; Heyes, 1993, 1994).

Since the observers did not have the opportunity to interact with the stimulus at the same time as the demonstrators, we can discard social facilitation (an indiscriminate increase in general activity as a result of observation: Zajonc, 1965) as a potential mechanism. Furthermore, in separating the demonstrator's apparatus from that of the observer by the use of duplicate cages we controlled for local enhancement, whereby the demonstrator's behaviour increases the probability that the observer will attend to the locale with which the demonstrator interacted (Thorpe, 1963). Instead, we need be concerned with four types of social learning, namely stimulus enhancement (Spence, 1937), imitation (Thorndike, 1898; Morgan 1900), goal emulation (Tomasello, 1990; Whiten and Ham, 1992), and response facilitation (Byrne, 1994).

For our purposes, stimulus enhancement refers to the demonstrator's behaviour increasing the probability that the observer will attend to/interact with stimuli of the same physical type as those with which the demonstrator interacted. Imitation refers to cases in which, as a result of observation, the observer acquires a novel behaviour from the repertoire of the demonstrator. Goal emulation refers to the observer duplicating the results of the demonstrator's behaviour (the goal) but not its methods. Response facilitation refers to the increased probability of the observer performing a particular behaviour (already in its repertoire) as a result of observing the demonstrator performing the same behaviour.

Since observers were facilitated to approach the apparatus, and to touch it once in proximity to it, one mechanism at work here appears to be stimulus enhancement, whereby the observer completes the task by simple trial and error learning but learns from the demonstrator to direct its appetitive actions towards the apparatus. However, since the categories of social learning are not mutually exclusive it is possible, in principle, that the demonstrator played several roles simultaneously. Thus the possibility remains that, through its behaviour at the string, the demonstrator increased the probability that the observer would interact with the apparatus (stimulus enhancement), and furthermore, may have acted as a model regarding the actions necessary to obtain the food item (imitation). Unfortunately, in recording simply the latency to perform the various behavioural components necessary to succeed on the task, we are ill-prepared to confirm the presence of imitation. As described by Whiten and Ham (1992) for the observer-demonstrator paradigm used here, "while speed of learning can be easily and objectively measured, it is insufficient to discriminate between stimulus enhancement and imitation" (p. 242). In order to distinguish explicitly

between these two categories of social learning, one must use a 'two-action method' (Dawson and Foss, 1965), where there are two possible ways in which to complete the experimental task and one looks to see if the observers tend to complete the task using the method which their demonstrators used, in preference to the alternative method. Using this technique, Bugnyar and Huber (1997) have found common marmosets (*Callithrix jacchus*) able to imitate their conspecifics either pushing or pulling a pendulum door to open a wooden box (or at least 'mimic', excluding insight or any perception or understanding of how the copied behaviour is designed to bring about the goal). The task we are concerned with here could be completed successfully in one way only and so cannot provide evidence for imitation. Furthermore, because of an absence of data on differences in action pattern, we are also unable to draw any conclusions regards goal emulation.

With regard to our remaining mechanism, response facilitation, it is interesting to note that, although observers were facilitated to approach and to touch the string, they were also facilitated to complete the task once having done so. This suggests that they learned something about the actions necessary to succeed on the task and obtain the food item, apart from any intrinsic orienteering to the stimulus. So, in addition to having their attention and subsequent manipulations directed to the apparatus, the observers were also selectively enhanced to apply particular matching behaviours already in their repertoire (response facilitation) to solve the problem rapidly, giving the impression of imitation. Byrne (1995) writes that such a combination of stimulus enhancement and response facilitation is a powerful one, quite apart from the possibility of goal emulation.

We appear, then, to have an ecologically-orientated example of stimulus enhancement and response facilitation in two species of *Saguinus*. In past experiments, captive monkeys have often failed to show forms of social learning such as these (see Whiten and Ham, 1992: Table IV). The slow rate of learning described in previous captive studies may reflect irrelevance of the testing environment to the monkeys natural habitat, pronounced hierarchical differences among dyads, or may be a result of traditional fixed-trial procedures which allow only limited periods of interaction between individuals. In the field, where animals have the freedom to interact continuously, learning processes may be much more rapid (Galef, 1976).

Other reports of rapid learning exist for captive *Saguinus*. Hardie (1995) found that, after a single trial, troops of *S. fuscicollis* and *S. labiatus* respond differentially to objects paired with food and those not paired with food. Furthermore, this information could be retained for a

period of at least 7 weeks and could be transferred between the species. Similar swift learning was again demonstrated in an eight-member family of *S. fuscicollis* (Menzel and Juno, 1982, 1984) who, on a single exposure to objects associated with food, increased their frequency of approach to those objects on the next trial. Such rapid learning in tamarins may reflect species-specific propensities for particular kinds of learning or learning capacity in relation to social structure (Goodall, 1973; Itani and Nishimura, 1973; Cambefort, 1981), social dynamics (Coussi-Korbel and Frigaszy, 1995), or to the distribution pattern of major food resources (Milton, 1988). For example, Coussi-Korbel and Frigaszy (1995) suggest that, squirrel monkeys (*Saimiri at al.*) would be less likely than tamarins to acquire information from one-another about the non-social environment, because, owing to competing attentional demands arising from a modest hierarchical organisation, they are less likely to focus their attention upon one-another for more than brief moments. This brings us back to the proposition that the transmission of information through ongoing behaviour will be greater in species exhibiting a high degree of tolerance and co-ordination in time and space. These are characteristics of both single and mixed-species tamarin troops.

Tamarins spend a great deal of their time foraging for food (*S. fuscicollis*, for example, are reported to spend around 60 % of their daily activity period foraging for plant food and insects: Soini, 1987; Terborgh, 1983). The identification and acquisition of food is likely to constitute one of their greatest environmental challenges. Foraging in a cohesive troop can, through social learning, convey important information about the availability, location, stimulus characteristics and method of acquisition of food to individual members. Mixed-species troop formation, by increasing troop size, is likely to facilitate the transfer of socially learned foraging information accordingly.

ACKNOWLEDGEMENTS

Part of the results in this paper were presented in a symposium at the XVIIth Congress of the International Primatological Society, Antananarivo, Madagascar, 1998. We thank Lesley Rogers and Hilary Box for inviting us to contribute. The research was supported by a University of Stirling studentship awarded to M.J. Prescott. We gratefully acknowledge the staff at Belfast Zoological Gardens for the opportunity to conduct the research and for maintaining the study animals. We also thank Scott Hardie and Lesley Rogers for critical comments on the manuscript.

REFERENCES

- Adams-Curtis, L.E., & Fragaszy, D.M. (1995). Influence of a skilled model on the behaviour of conspecific observers in tufted capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, 37, 65-71.
- Beauchamp, G., & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata*. *Animal Behaviour*, 41, 247-253.
- Buchanan-Smith, H.M. (1989). The social organisation and mating system of the red bellied tamarins (*Saguinus labiatus labiatus*); Behavioural observations in captivity and in the wild. Unpublished Ph.D. thesis, University of Reading, Reading.
- Buchanan-Smith, H.M. (1990). Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *American Journal of Primatology*, 22, 205-214.
- Buchanan-Smith, H.M. (1991). Encounters between neighbouring groups of tamarins in northern Bolivia. *Primate Report*, 31, 95-99.
- Buchanan-Smith, H.M. (1999). Tamarin polyspecific associations: Forest utilisation and stability of mixed-species groups. *Primates*, 40, 233-247.
- Buchanan-Smith, H.M., & Hardie, S.M. (1997). Tamarin mixed-species groups: An evaluation of a combined captive and field approach. *Folia Primatologica*, 68, 272-286.
- Bugnyar, T., & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour*, 54, 817-831.
- Byrne, R.W. (1994). The evolution of intelligence. In P.J.B Slater & T.R. Halliday (Eds.), *Behaviour and Evolution* (pp. 223-265). Cambridge: Cambridge University Press.
- Byrne, R.W. (1995). *The Thinking Ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
- Caine, N.G. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In Rylands, A.B. (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 200-219). Oxford: Oxford University Press.
- Caine, N.G., & Stevens, C. (1990). Evidence for a 'monitoring' call in captive red-bellied tamarins. *American Journal of Primatology*, 22, 251-262.
- Caine, N.G., Addington, R.L., & Windfelder, T.L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, 50, 53-60.
- Cambeftort, J.P. (1981). Comparative study of culturally transmitted patterns of feeding habits in the Chacma baboon (*Papio ursinus*) and the vervet monkey (*Cercopithecus aethiops*). *Folia Primatologica*, 36, 243-263.
- Castro, R., & Soini, P. (1977). Field studies on *Saguinus mystax* and other callitrichids Amazonian Peru. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp.73-78). Washington D.C.: Smithsonian Institution Press.
- Coates, A., & Poole, T.B. (1983). The behaviour of the callitrichid monkey, *Saguinus labiatus*, in the laboratory. *International Journal of Primatology*, 4, 339-371.
- Coussi-Korbel, S., & Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441-1453.
- Dawson, B.V., & Foss, B.M. (1965). Observational learning in budgerigars. *Animal Behaviour*, 13, 470-474.

- Fragaszy, D.M., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviours in capuchin monkeys. *Folia Primatologica*, 54, 155-165.
- Galef, B.G. (1976). Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Beer (Eds.), *Advances in the Study of Behavior*, Vol. 6. (pp. 77-100). New York: Academic Press.
- Galef, B.G. (1988). Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In T.R. Zentall & B.G. Galef (Eds.), *Social Learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale, New Jersey: Erlbaum.
- Garber, P.A. (1986). The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *S. fuscicollis*). *American Journal of Primatology*, 10, 155-170.
- Garber, P.A. (1987). Foraging strategies among living primates. *Annual Review of Anthropology*, 16, 339-364.
- Garber, P.A. (1988a). Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica*, 20, 100-106.
- Garber, P.A. (1988b). Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour*, 105, 18-34.
- Garber, P.A. (1993). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology*, 14, 145-166.
- Giraldeau, L.A., & Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour*, 35, 387-394.
- Goldizen, A.W. (1987). Tamarins and marmosets: communal care of offspring. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., & Struhsaker, T.T. (Eds.), *Primate Societies* (pp. 34-43). Chicago: University of Chicago Press.
- Goldizen, A.W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behavioural Ecology and Sociobiology*, 24, 79-89.
- Goodall, J. (1973). Cultural elements in a chimpanzee community. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 144-184). Basel: Karger.
- Hardie, S.M. (1995). The behaviour of mixed-species tamarin groups (*Saguinus labiatus* and *Saguinus fuscicollis*). Unpublished Ph.D. thesis, University of Stirling, Stirling.
- Hardie, S.M. (1997). Exhibiting mixed-species groups of sympatric tamarins (*Saguinus* spp.) at Belfast Zoo. *International Zoo Yearbook*, 35, 261-266.
- Hardie, S.M. (1998). Mixed-species tamarin groups (*Saguinus fuscicollis* and *Saguinus labiatus*) in northern Bolivia. *Primate Report*, 50, 39-62.
- Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini)*, Vol 1. Chicago: University of Chicago Press.
- Heymann, E.W. (1987). A field observation of predation on a moustached tamarin (*S. mystax*) by an anaconda. *International Journal of Primatology*, 8, 193-195.
- Heymann, E.W. (1990). Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *American Journal of Primatology*, 21, 115-127.

- Heymann, E.W. (1997). The relationship between body-size and mixed-species troops of tamarins (*Saguinus* spp.). *Folia Primatologica*, 68, 287-296.
- Heymann, E.W., & Sicchar-Valdez, L.A. (1988). Interspecific social grooming in a mixed troop of tamarins, *S. mystax* and *S. fuscicollis* (Platyrrhini: Callitrichidae), in an outdoor enclosure. *Folia Primatologica*, 50, 221-225.
- Heymann, E.W., Sicchar V., L.A., & Tapia, R.J. (1996). Experiences with mixed-species housing of tamarins, *S. fuscicollis* and *S. mystax* (Primates: Callitrichidae), in an outdoor enclosure. *Zoologischer Garten NF*, 66, 381-390.
- Heyes, C.M. (1993). Imitation, culture and cognition. *Animal Behaviour*, 46, 999-1000.
- Heyes, C.M. (1994). Social learning in animals: categories and mechanisms. *Biological Review*, 69, 207-231.
- Itani, J., & Nishimura, A. (1973). The study of infra-human culture in Japan. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 26-50). Basel: Karger.
- Klein, L.L., & Klein, D.J. (1973). Observations of two types of Neotropical primate intertaxa associations. *American Journal of Physical Anthropology*, 38, 649-654.
- Krebs, J.R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian Journal of Zoology*, 51, 1275-1288.
- Laland, K.N., Richerson, P.J. & Boyd, R. (1993). Animal social learning: towards a new theoretical approach. In P.P.G. Bateson, P.H. Klopfer & N.S. Thompson (Eds.), *Perspectives in Ethology*, Vol. 10 (pp. 249-277). New York: Plenum Press.
- Mayer, K.E., Blum, C.A., & Caine, N.G. (1992). Comparative foraging styles of tamarins and squirrel monkeys. *American Journal of Primatology*, 27, 46. (Abstract).
- Menzel, E.W., & Juno, C. (1982). Marmosets (*Saguinus fuscicollis*): Are learning sets learned? *Science*, 217, 750-752.
- Menzel, E.W., & Juno, C. (1984). Are learning sets learned? Or: Perhaps no nature-nurture issue has any simple answer. *Animal Learning and Behaviour*, 12, 111-115.
- Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence. In R.W. Byrne & A. Whiten (Eds.), *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans* (pp. 285-305). Oxford: Oxford University Press.
- Moody, M.F., & Menzel, E.W. (1976). Vocal communication in marmosets (*Saguinus fuscicollis*). *Folia Primatologica*, 25, 73-94.
- Morgan, C.L. (1900). *Animal Behaviour*. London: Edward Arnold.
- Noldus (1993). *The Observer: System for collection and analysis of observational data*. Wageningen, Netherlands: Noldus Information Technology b.v.
- Norconk, M.A. (1986). Interactions between primate species in a neotropical forest: mixed species troops of *Saguinus mystax* and *S. fuscicollis* (Callitrichidae). Unpublished Ph.D. thesis, University of California, Los Angeles.
- Norconk, M.A. (1990). Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. *American Journal of Primatology*, 21, 129-146.
- Peres, C.A. (1991). Ecology of mixed species groups of tamarins in Amazonian terra firme forests. Unpublished Ph.D. thesis, University of Cambridge, Cambridge.
- Peres, C.A. (1992a). Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. *Behaviour*, 123, 220-246.
- Peres, C.A. (1992b). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. *Behavioural Ecology and*

Sociobiology, 31, 339-347.

- Peres, C.A. (1993). Anti-predator benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica*, 61, 61-76.
- Peres, C.A. (1996). Food patch structure and plant resource partitioning in interspecific associations of Amazonian tamarins. *International Journal of Primatology*, 17, 695-723.
- Pook, A.G., & Pook, G. (1982). Polyspecific association between *Saguinus fuscicollis*, *Saguinus labiatus*, *Callimico goeldii*, and other primates in north-western Bolivia. *Folia Primatologica*, 38, 196-216.
- Ramirez, M. (1989). Feeding ecology and demography of the moustached tamarin, *Saguinus mystax*, in northeastern Peru. Unpublished Ph.D. thesis, City University of New York, New York.
- Rubenstein, D.I., Barnett, R.J., Ridgley, R.S., & Klopfer, P.H. (1977). Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. *Ibis*, 119, 10-21.
- Snowdon, C.T., & Soini, P. (1988). The tamarins, genus *Saguinus*. In R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho, & G.A.B. Fonesca. (Eds.), *Ecology and Behavior of Neotropical Primates*, Vol 2. (pp. 223-298). Washington D.C: WWF.
- Soini, P. (1987). Ecology of the saddle-back tamarin, *Saguinus fuscicollis illigeri* on the Rio Pacaya, northeastern Peru. *Folia Primatologica*, 49, 11-32.
- Spence, K.W. (1937). Experimental studies of learning and higher mental processes in infra-human primates. *Psychological Bulletin*, 34, 806-850.
- Terborgh, J. (1983). *Five New World Primates: A study in comparative ecology*. Princeton, New Jersey: Princeton University Press.
- Thorndike, E.L. (1898). Animal intelligence: An experimental study of the associative process in animals. *Psychological Review Monograph*, 2 (Suppl. 4), 1-109.
- Thorpe, W.H. (1963). *Learning and Instinct in Animals*. London: Methuen.
- Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S.T Parker & K.R.G. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative developmental perspectives* (pp. 274-311). Cambridge: Cambridge University Press.
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In P.J.B. Slater, J.S. Rosenblatt, C. Beer & M. Milinski (Eds.), *Advances in the Study of Behavior*, Vol. 21 (pp. 239-283). New York: Academic Press.
- Weigel, P.D., & Hanson, E.V. (1980). Observational learning and the feeding behavior of the red squirrel *Tamiasciurus hudsonicus*: the ontogeny of optimisation. *Ecology*, 61, 213-218.
- Windfelder, T.L. (1997). Polyspecific association and inter-specific communication between two Neotropical primates: Saddle-back tamarins (*Saguinus fuscicollis*) and emperor tamarins (*Saguinus imperator*). Unpublished Ph.D. thesis, Duke University, Durham.
- Yoneda, M. (1981). Ecological studies of *Saguinus fuscicollis* and *S. labiatus* with reference to habitat segregation and height preference. *Kyoto University Overseas Research Report of New World Monkeys*, 2, 43-50.
- Yoneda, M. (1984a). Comparative studies on vertical separation, foraging behavior and travelling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in Northern Bolivia. *Primates*, 25, 414-422.

- Yoneda, M. (1984b). Ecological study of the saddle backed tamarin (*Saguinus fuscicollis*) in northern Bolivia. *Primates*, 25, 1-12.
- Zajonc, R.B. (1965). Social facilitation. *Science*, 149, 269-274.
- Zentall, T.R., & Galef, B.G. (1988). *Social Learning*. Hillsdale, New Jersey: Erlbaum.

FACTORS ASSOCIATED WITH EXPLORATION IN MARMOSETS: AGE, GENDER AND HAND PREFERENCE

L. J. Rogers

University of New England, AUSTRALIA

ABSTRACT: Age, hand preference and gender are shown to be associated with exploration behaviour performed by *Callithrix jacchus*, depending on the context in which the marmosets are tested. When each marmoset was tested alone in a novel environment, hand preference had a significant effect on exploration: right-handed marmosets explored more actively than left-handed ones. This difference is probably related to hemispheric specialisation for processing novel stimuli and controlling emotional responses. Age and gender were found to have no significant effect on exploration in this context. When the marmosets were tested in the social groups and by placing novel objects in their home cages, both hand preference and age influenced approach and interaction with the stimuli, but again gender had no significant effect. Solving a novel problem in the home cage was influenced only by age, or related social dominance, and not by gender or hand preference. The implications of these results to behaviour of wild marmosets and other species are discussed.

This paper will discuss the influences of age, gender and hand preference on responses to novelty in the common marmoset, *Callithrix jacchus*. It will show that the relative contribution of each of these factors varies with the context in which the exploration is taking place, specifically whether the marmosets are in social groups in a familiar setting or in isolation in a novel setting.

Age has been shown to affect exploration in primates in many taxa (e.g. Menzel and Menzel, 1979). Typically juveniles are more likely to approach novel stimuli than are adults and they are more active than adults when placed in a novel setting. Menzel and Menzel (1979) found that juvenile saddle-backed tamarins (*Sanguinus fuscicollis*) approach a novel stimulus in the home cage sooner than do adults, and they spend

Address correspondence to L. J. Rogers, School of Biological Sciences, University of New England, Armidale, NSW 2351, Australia.

more time attending to it than adults. Attention to a novel stimulus may involve active approach and interaction, but it may also involve visual investigation from a distance, and this form of visual exploration might be achieved by head cocking, rotation of the head around the longitudinal axis of the body while orienting toward a stimulus. Head cocking in primates appears to be a form of visual exploration because it occurs more frequently when novel stimuli are presented (Rogers, Stafford & Ward, 1993). Since head cocking is more common in juveniles than adults, as Menzel (1980) found in squirrel monkeys, we may use this specific behaviour as another indication that juveniles pay more attention to novel stimuli than do adults.

Gender is also known to influence some aspects of exploration in primates, as well as other species. Typically females show more exploration than males, although this is not the case for vigilance (Box, 1999). Female primates, across widely different taxa, also acquire new behaviour patterns more readily than males (Kappeler, 1987; Bachevalier, Hagger & Bercu, 1989), suggesting that females may be more attentive to novel situations than males. In galagos, females head cock more frequently than males when presented with a novel stimulus (Rogers et al., 1993), indicating that they pay more attention to novel stimuli than males.

Recently, hand preference has been shown to influence responses to novelty (Hopkins and Bennett, 1994). Left- and right-hand preferring chimpanzees were given the opportunity to explore novel toys. Hopkins and Bennett (1994) found that the right-hand preferring subjects approached the novel objects and interacted with them more than the left-hand preferring subjects. Hence approach and exploration may be related to greater control by the left hemisphere (which controls the right hand) than by the right hemisphere (which controls the left hand). Hand preference has also been shown to influence the responses of bushbabies (*Otolemur garnettii*) in a novel environment. Watson & Ward (1996) found that left-hand preferring subjects were more active (scored as jumping and sector crossing) than the right-hand preferring ones. This may indicate that left-hand preferring bushbabies explore the novel environment more than right-hand preferring ones, and this would be opposite to the result obtained with chimpanzees. If so, the difference between these two results may depend on the species tested or the conditions of the testing. The bushbabies were, for example, tested singly, whereas the chimpanzees were tested in their social group. It is known that social conditions influence the responses to novelty (Fragaszy & Mason, 1978). Age and sex differences between

subjects and studies need to be considered also, as well as species differences.

The relationship between hand-preference and exploration is likely to reflect differential use of the left and right hemispheres. A subject with a consistent preference to use the right hand may have a tendency towards greater use of the left hemisphere than the right in most situations. The converse may be the case for subjects with a preference to use the left hand. If so, hand preference may reflect more general aspects of cognitive function, since each of the hemispheres is specialised to carry out different kinds of information processing and to control different functions.

Davidson (1992) has suggested that approach behaviour may be associated with greater activation of the left hemisphere and avoidance by greater activation of the right hemisphere. In humans, the right hemisphere is considered to be specialised for processing negative emotional stimuli and the left hemisphere for processing positive emotional stimuli (Bogen, 1985). The same may be true in nonhuman primates since there is evidence that the right hemisphere is involved in fear and aggressive responses. Specialisation of the left hemisphere for positive emotions (and approach) and the right hemisphere for negative emotions (and avoidance) may be the reason why right-hand preferring chimpanzees were more likely to approach the novel objects and interact with them. However, more species of primates will need to be tested to confirm this hypothesis.

Casparid and Dunbar (1996) have found that gelada baboons are more likely to direct agonistic responses to a conspecific on their left side than on their right side, indicating right hemispheric control. Hauser (1993) has shown that, in rhesus monkeys, fear responses are expressed more strongly on the left side of the face, also indicating control by the right hemisphere. In the common marmoset also, fear expressions involve greater movement of the muscles on the left side of the face (Hook-Costigan & Rogers, 1998a). In fact, when marmosets make a mobbing call, they open the left side of their mouth more widely than the right and the reverse occurs when they make a contact twitter call. These data indicate that the right hemisphere is specialised for aggressive and fear responses. It may, therefore, process negative emotions. The left hemisphere, by contrast, may be specialised for contact and approach, a more positive emotional state. That is why hand preference was taken into account in the analyses of exploration by the common marmoset to follow.

Common marmosets are excellent subjects to test the potential

influence of hand preference on responses to novelty because approximately half of the subjects in a group are right-hand preferring and the other half left-hand preferring (Box, 1977; Hook-Costigan & Rogers, 1997). Although their hand-preferences vary with the task to which they are applied (Hook-Costigan & Rogers, 1995), individuals use the same hand consistently over time to pick up pieces of food from the ground and take them to their mouth to feed (Hook-Costigan & Rogers, 1997). Hence, if hand preference reflects differential activity of the hemispheres, half of the individuals may have greater activity of the left hemisphere (the right-handed subjects) and the other half may have greater activity of the right hemisphere (the left-handed subjects). These biases may reflect different ways of processing information and reacting to stimuli. In fact, it is known that marmosets have differential specialisation of the left and right hemispheres, as shown by a group bias to view neutral stimuli with the right eye (Hook-Costigan & Rogers, 1998b; Hook-Costigan, 1999) and by group bias in asymmetry of facial expressions (Hook-Costigan & Rogers, 1998a). Therefore it was predicted that right-hand preferring marmosets might show more exploration behaviour in a novel environment and they might approach novel stimuli more readily than left-hand preferring marmosets.

Three contexts were used to test exploration in the marmosets in captivity: 1) exploration of a novel environment in isolation, 2) exploration of novel objects in the home-cage together with the familiar social group, and 3) approach and attention to solving an unfamiliar problem in isolation but still in a section of the home-cage. Although it is recognised that numerous factors may influence the responses of the marmosets in these contexts, including early experience (as described by Kaplan & Rogers, 1999), only age, gender and hand preference were considered here.

1. EXPLORATION ALONE IN A NOVEL ENVIRONMENT

METHODS

Subjects and Housing

Twenty, adult (21 to 68 months) common marmosets (12 females and 8 males) of the colony at the University of New England were tested by placing them singly into an unfamiliar room (approximately 3m square). The room contained a variety of novel objects on which

they could climb or which they could manipulate. The objects included branches, ropes, wire-mesh and bamboo structures for climbing, a variety of toys and strips of hanging cloth. Some of the objects were freshly scented with banana or blueberry odour before each test. A basket of straw from the home cage was also suspended in the room to provide a familiar odour.

Procedure

Each marmoset was taken into the room in its nesting box and then the door of this box was opened and the experimenter left the room. For the next hour the behaviour of the marmosets was recorded by videotaping through two one-way mirrors. The mirrors themselves were an aspect of the novelty of the room. Playback of the videotapes provided scores of latency to leave the nesting box to enter the unfamiliar environment, number of leaps (feet and hands off the substrate together), parallax movements of the head from side to side (used in perceiving depth), touches of the objects, head cocking movements and number of objects touched. The marmosets could return to the nesting box if they wanted to, and total time spent in the box was also recorded.

Analysis

The data were analysed for the effects of gender, age and hand preference, and these results have been reported in detail in Cameron and Rogers (1999). The hand preference of each subject had been determined 1 month prior to testing. It was calculated from 100 scores of picking up food and taking it to the mouth. The subject was in a relatively relaxed state in the home cage. No more than 15 scores were recorded on any day and runs or bouts were avoided by not scoring repeated taking of the same piece of food to the mouth. The hand preference was considered to be significant on the basis of *z*-score analysis (Cameron & Rogers, 1999). There were no subjects without a significant hand preference. As an additional check of the hand preference scored, the preferences scored one month prior to testing were correlated with data collected for the same individuals and in the same manner 10 months prior to that time. There was a strong positive correlation (Pearson correlation, $r = .91$, $p < .0005$), showing the consistency of hand preference for each individual. In the group tested there were 5 right-handed males, 3 left-handed males, 3 right-handed

females and 9 left-handed females. The statistical analyses took into account the variation in group sizes.

RESULTS AND DISCUSSION

The latency scores differed significantly in the left- and right-handed subjects (for details of statistical results see Cameron & Rogers, 1999). All but one of the right-handed subjects left the nesting box to enter the unfamiliar room in less than 100 seconds. This was true also of half the left-handed subjects, but the remaining left-handed subjects formed a second cluster with latencies in excess of 100 seconds (range of 110 to 250 secs).

It will be noted that none of the latencies were long enough to have a significant effect on behaviour in the room because 1 hour was allowed to collect those scores. Hand preference had a separate and significant effect on behaviour in the room. The right-handed marmosets performed twice as much leaping and twice as many parallax movements and touches of objects as did the left-handed marmosets (Fig. 1; for details of statistics see Cameron & Rogers, 1999). In addition, they touched more than twice the number of different objects than did the left-handed ones. These results are consistent with the prediction outlined above. Age at testing and gender had no significant effects on these particular behaviours and, furthermore, gender had no significant effect on any of the behaviours scored.

Head cocking, however, occurred at the same levels in the right- and left-handed subjects. Although it was not influenced by hand preference, head cocking was affected by age. Older marmosets had lower scores of head cocking than younger ones ($r = -.66$, $p = .01$, Pearson correlation). Time spent in the nesting box also had no relationship to hand preference but correlated negatively with age ($r = -.55$, $p = .01$). Therefore age affected some of the behaviours that can be termed exploratory but not the same behaviours as hand preference.

The fact that right-handed subjects perform more visual exploration by parallax movements than left-handed subjects but both groups perform the same amount of head cocking deserves further mention. It was considered possible that the extra parallax movements of the right-handers stems from the fact that they explore the novel environment more actively by leaping than do the left handers. Leaping requires accurate assessment of distance and parallax movements would provide

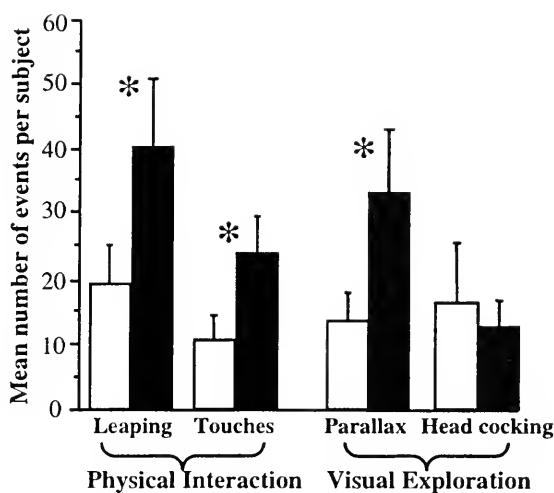


Figure 1. Exploration alone in a novel environment. The mean number of events of each behaviour has been plotted with standard errors indicated. The white and black bars are for left-handed and right-handed subjects respectively. The asterisks indicate significant differences between the scores for left- and right-handed subjects. This figure has been adapted from Cameron & Rogers (1999). Note that right-handed subjects perform more active exploration of the novel environment than left-handed subjects. They also perform more visual exploration by parallax movements than the left-handers but both groups perform similar amounts of head cocking.

information for this. Head cocking, by contrast, might be seen as a way of visually exploring the new environment without physically interacting with the novel stimuli. It might be 'exploration at a distance' and, if so, could explain why left-handed subjects engage in it as much as right-handed subjects.

The number of parallax movements performed does, in fact, correlate with the number of leaps (Spearman correlation, $r = .42$, $p = .023$) but there is a tendency for the same relationship to hold between head cocking and leaping ($r = .42$, $p = .063$). In fact, head cocking and parallax correlated strongly in the left-handed subjects ($r = .82$, $p = .002$) but not in the right-handed subjects ($r = .31$, $p = .42$). This disassociation between head cocking and parallax movements in the right handers indicates that they are separate ways of actively exploring the novel environment. However, parallax did not correlate

significantly with leaping in the right handers ($r = .33, p = .38$), whereas it did in the left handers $r = .63, p = .039$). The extra leaping performed by the right-handed subjects, therefore, is not associated with extra parallax movements. This examination of the data fails to provide strong support for the hypothesis about head cocking being exploration at a distance and parallax being an aspect of interactive exploration, but it does show that the two types of visual exploration are separate to at least some degree.

2. EXPLORATION OF NOVEL OBJECTS IN THE HOME CAGE AND WITH THE SUBJECT'S SOCIAL GROUP

METHODS

Subjects and Procedure

Nineteen of the same subjects were also tested by presenting novel stimuli to them in their home-cage groups (tests conducted 1 year prior to the above). The marmosets were tested in familiar, unisex groups of 2 to 4 subjects. A platform on which novel objects were presented was placed in the home cage. The novel stimuli presented on the platform were either potential food items, presented inside 4 glass Petrie dishes (live cockroaches, plastic models of insects or a small mirror inside each dish, in which the marmosets could see their own image), or they were potential predators, simply placed on the table (a coiled, model snake or a model resembling two rearing snakes inside a jar). The stimuli were presented for one hour on each of four consecutive days separated by intervals of 7 days, but only the data for the first day of presentation will be considered here because only then were the stimuli entirely novel. Only one stimulus type was presented at a time and the order of presentation was randomised. A video camera directed at the platform was used to record the responses of the marmosets to the novel stimuli. The number of periods spent by each subject on the platform was determined and also the total time spent on the platform.

Analysis

As these data have not yet been submitted for publication elsewhere (Rogers, Hook-Costigan & Johnston, in preparation), they will be presented in somewhat more detail here than the data for the

other experiments. However, as total time spent on the platform correlated with the number of periods on the platform, only the latter will be presented. The scores of number of periods on the platform were analysed first for any effects of gender. As no significant effect of gender was found, the data for males and females together was examined using the log-transformed data in a 3-way ANOVA, with stimulus type as a repeated measure together with the factors age (subadult versus adult) and hand preference (left or right). The age dividing subadults from adults was 20 months, and there were 8 subadults (4 left-handed and 4 right-handed) and 10 adults (6 left-handed and 4 right-handed). One subject was eliminated from the analysis because it was ambipreferent for picking up food at this time, although later it did develop a hand preference.

RESULTS AND DISCUSSION

There were significant main effects of stimulus ($F_{4,70} = 13.9$, $p < 0.0001$), age ($F_{1,70} = 14.2$, $p = 0.0003$) and hand preference ($F_{1,70} = 5.9$, $p = 0.018$). The only significant interaction was between age and stimulus ($F_{4,70} = 3.6$, $p = 0.0097$). Subadults scored almost twice as many periods on the platform as did adults. This was true for all stimuli except the rearing snakes, which elicited the highest levels of fear. Hand preference for food holding was significantly associated with the number of periods on the platform: right-hand preferring individuals had higher scores than the left-hand preferring individuals.

Figure 2 illustrates the effect of age on investigation of the novel stimuli. It shows that subadults had higher scores for the number of periods spent on the platform than adults. This was the case for all of the stimuli, except the model of rearing snakes and there was only a trend towards this difference for the coiled snake. The rearing-snakes model elicited a distinctly different set of responses from the marmosets than did any of the other stimuli. First, as can be seen in Figure 2, the marmosets were much less likely to approach this stimulus than any of the other stimuli. Second, only this stimulus evoked the mobbing (tsik) calls. In other words, the marmosets showed fear responses to this stimulus, whereas this was not the case for any of the other stimuli. None of the other stimuli evoked the types of vocalisations characteristic of a state of fear (tsik, egg or ock calls). The rearing-snakes model has been referred to by Kaplan and Rogers (1999a, 1999b) and approach to this stimulus was found to depend on

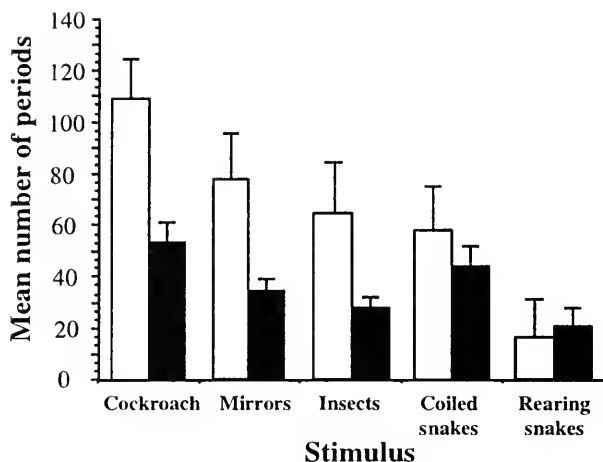


Figure 2. Exploration of novel objects in the home cage: the influence of age. The number of periods spent on the platform exploring each set of novel stimuli is plotted as means and standard errors for the subadults (white bars) and adults (black bars). Note that subadults investigate all of the stimuli, apart from the rearing snake model, more than the adults.

the amount of anogenital licking received by the marmoset during the first 2 months of life. Age did not have any influence on the responses to this particular stimulus.

The influence of hand preference on the number of periods spent on the platform is shown in Figure 3. Overall the marmosets with a right-hand preference investigated the novel stimuli more than the left-hand preferring marmosets. This result is consistent with the fact that right-handed marmosets explored the novel room more actively than the left-handed ones (see above). The only stimulus for which this relationship was not true was the coiled snake (Fig. 3), although this result was caused by the lumping of scores for adults and subadults. The relationship between increased exploration and hand preference was stronger for subadults than adults: hence the significant interaction between age and hand preference mentioned above. As shown in Figure 4, right-handed subadults investigated all of the novel stimuli to a greater extent than left-handed subadults.

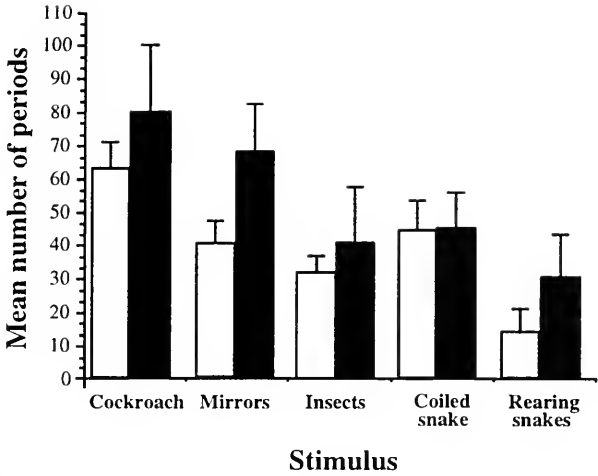


Figure 3. Exploration of novel objects in the home cage: the influence of hand preference. The data for subadults and adults combined are plotted as in Figure 2. The white bars indicate the scores for marmosets preferring to use the left hand during feeding and the black bars represent those preferring to use the right-hand.

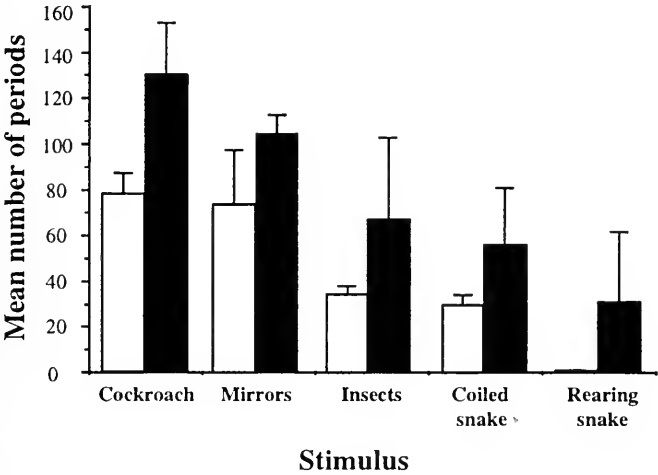


Figure 4. Exploration of novel objects in the home cage: the influence of hand preference for subadults only. The white bars represent the left handers and the black bars the right handers.

3. AN UNFAMILIAR PROBLEM IN THE HOME CAGE

METHODS

Procedure

Problem solving in the home cage was also scored for the same 20 subjects, approximately 3 months after they had been tested in the unfamiliar room (see Section 1 above). In this case, the marmoset being tested was partitioned off from the other members of its social group in a section of the home cage. There it was allowed 30 minutes to solve a novel problem. The problem was to slide a horizontal sheet on which a meal worm had been placed so that the worm fell through a hole in the middle of the sheet and so dropped to the bottom of a transparent cylinder from which it could be retrieved by the marmoset (Cameron & Rogers, 1999). Retrieval required the marmoset to reach through a small opening at the bottom of the cylinder. Once the meal worm had been retrieved and eaten, another worm was placed on the sliding sheet and a new trial could begin. The following were scored: the latency to approach the apparatus, total time spent on the platform interacting with the apparatus and the number of times the sliding sheet was successfully manipulated so that the marmoset could obtain the meal worm.

RESULTS AND DISCUSSION

The results have been published in detail by Cameron and Rogers (1999) and so will be summarised briefly here. There were no significant main effects of gender or hand preference on any of the behaviours measured, and there were no significant interactions with either of these factors. Age, however, did influence the time spent on the platform attending to the apparatus and the number of successful manipulations of the sliding sheet. Both of these behaviours correlated positively with age: the older marmosets were more successful than the younger ones in solving the problem. This result is inconsistent with the fact that younger marmosets pay more attention to novel stimuli presented in the home cage (see above). In the study reported here, there was no effect of age on the latency to approach the apparatus but older marmosets paid more attention to solving the problem.

The role of age in problem solving was further investigated. It was considered possible that the older marmosets may be more successful in solving the problem because they were more motivated to feed or because they were in a superior social position and less distracted by the nearby presence of other members of their group. Therefore competition for obtaining a favoured food was scored. A small piece of banana was placed on the wire wall of the home cage and the marmoset that obtained it was recorded. This was repeated for 100 scores per cage. Each individual was assigned as being 'dominant' or 'subordinate' depending on its relative success in obtaining the banana, although it is recognised that these labels are rather superficial and may have little to do with any broad assessment of social position. The accuracy of this categorisation was also limited by the fact that the marmosets were tested only with their own social group and only one individual per group was assigned as dominant, the rest being considered as subordinate. It was not possible to test each subject against every other subject because this would have disrupted the social groups and may have caused fighting and injury. In fact, even if it had been possible to test each individual against all others, the scores obtained would not have been particularly relevant because marmosets do not form simple hierarchies (Ferrari & Lopes Ferrari, 1989; Rothe & Keonig, 1991).

There was no significant effect of dominance on latency to approach the apparatus but dominant subjects spent more time attending to the apparatus and were more successful in solving the problem than the subordinate subjects. However, as dominant subjects tended to be older than subordinate ones (by some 10 months), the influences of age and dominance on problem solving could not be separated.

GENERAL DISCUSSION

In marmosets, the hand preference displayed by an individual while it is in a relaxed state feeding in the home cage and in its familiar social group may reflect the individual's baseline state of hemispheric control. In other words, a left-handed individual may have a baseline state in which the right hemisphere tends to be in charge of processing information and controlling behaviour, whereas the reverse may be the case for a right-handed individual. Therefore, although the hemisphere most active at any one time may change with context and state of arousal, there may be a tendency for some individuals to rely more strongly on activity of the right hemisphere and others on activity of the

left hemisphere. In turn, these differing dependencies on the left or right hemisphere may reflect differences in temperament and so determine the initial responses to novel stimuli (Table 1). For example, a left handed individual might begin a test in a more fearful state than a right-handed one and so be less likely to approach novel stimuli and interact with them. The hemisphere most active might well shift with time and experience in the testing situation but the resting or baseline state might set an initial bias of responding. Age and social position might override this effect of hand preference depending on context, as shown in the experiments reported here. It remains likely that gender would also have an effect on exploration in at least some contexts, although it had no significant influence on any responses scored in the tests used here.

Table 1. Summary of the results.

Factors influencing approach and exploration	Hand Preference	Age	Gender
Alone in a novel setting	+	-	-
Novel objects in familiar setting	+	+	-
Novel problem solving	-	+	-

Although the association between hand preference and exploration is modified by age and social position, it is interesting to speculate on whether differences in migration and territoriality may, at least in some species, depend on the distribution of hand preferences within the population, or on the presence or absence of handedness within the population. For example, a species (or a population) comprised of a majority of right-handed individuals may be more mobile and exploratory than one comprised of a majority of left-handed individuals, or one without handedness. In fact, tamarins (*Saguinus oedipus*) have a population bias of right handedness (King, 1995) and they are known to move daily over distances two times greater than those moved by marmosets (Tardif, Harrison & Simek, 1993), which have no population bias for handedness. There may, of course, be other explanations for this species difference but the presence or absence of handedness is now worth considering. It might be noted that lemurs are nocturnal and 'shy' and they are also left-handed at the population level (Ward, Milliken, Dodson, Stafford & Wallace, 1990). However, against this hypothesised association, Watson and Ward (1996) have found that left-handed bushbabies are more active in a novel environment. Further

research is needed to test whether any associations between handedness and species-typical behaviour are more than just coincidence. Even if this is the case, it does not imply that either handedness or exploration levels must be largely genetically determined, since early experience might affect the development of both characteristics.

Although there may be species or population differences in the association of handedness and exploration, any population will be made up of individuals with a range of levels of interactive exploration. Age, social position, hand-preference, gender and early experience may all affect the level of exploration that characterises each individual, depending on the context. The role of hand-preference is a newcomer to the list of factors that are associated with exploration and whether an individual is 'bold' or 'shy'. It is a factor that might now be considered in other species and may have application to the reintroduction of rare, related species to the wild. Depending on the environment to which captive-bred individuals are to be introduced, it might be advantageous to release left- or right-hand preferring individuals. Right-handed subjects might fare better than left-handed ones in environments that are constantly varying, and left-handed subjects might survive better than right-handed ones in environments that are more stable and where fixed territories can be held.

Psychologists have referred to a continuum from shyness to boldness in human behaviour, and some researchers of animal behaviour have done the same (Wilson, Clark, Coleman & Dearstyne, 1994). In fact, the data from humans suggests that extremely shy and extremely bold individuals are more stable (or inflexible) in their respective characteristics than individuals in the middle of the continuum. The latter are said to exhibit shyness or boldness depending on the context. It is not known whether hand preferences are in any way related to the extremes of shyness and boldness in humans, but the data discussed here for marmosets suggests that it would be interesting to test for an influence of hand preference on shyness versus boldness in humans. In fact, Watson and Ward (1996) have suggested that hand preference is related to shyness and boldness in prosimians and the same terms might also be used to describe the differences that Hopkins and Bennett (1994) found between left- and right-handed chimpanzees. Whether there is a continuum from shyness to boldness or, instead, two discrete categories exist might vary from species to species. Also, any tendency for one factor (e.g. hand preference) to polarise individuals into either of these two categories may be modified by another factor (e.g. age) that obscures this trend, depending on the context in which testing occurs.

ACKNOWLEDGEMENTS

The author acknowledges funding from the Australian Research Council (Special Investigator Award) for the research presented here. The work was also assisted by Rebecca Cameron, an Honours student, Dr Michelle Hook-Costigan, then a postgraduate student, and Dr Amy Johnston, a postdoctoral research assistant.

REFERENCES

- Bachevalier, J., Hagger, C. & Bercu, B.B. (1989) Gender differences in visual habit formation in 3-month-old rhesus monkeys. *Developmental Psychobiology*, 22, 585-599.
- Bogen, J.E. (1985). The callosal syndromes. In K.M. Heilman & E. Valenstein (Eds.), *Clinical Neuropsychology* (pp. 295-338). New York: Oxford University Press.
- Box, H. (1977). Observations on spontaneous hand use in the common marmoset (*Callithrix jacchus*). *Primates*, 18, 395-400.
- Box, H.O. (1999). Gender differences in marmosets and tamarins: Responses to food tasks. *International Journal of Comparative Psychology*, 12, 58-69.
- Cameron, R. & Rogers, L.J. (1999) Hand preference of the common marmoset (*Callithrix jacchus*), problem solving and responses in a novel setting. *Journal of Comparative Psychology*, 113, 1-9.
- Casperd, J.M. & Dunbar, R.I.M. (1996). Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. *Behavioural Processes*, 37, 57-65.
- Davidson, R.J. (1992). Emotion and affective style: Hemispheric substrates. *Psychological Science*, 3, 39-43.
- Ferrari, S.F. & Lopes Ferrari, M.A. (1989). A re-evaluation of the social organisation of the Callitrichidae, with reference to the ecological differences between genera. *Folia Primatologica*, 52, 132-147.
- Fragaszy, D.M. & Mason, W.A. (1978). Responses to novelty in Saimiri and Callicebus: Influence of social context. *Primates*, 19, 311-331.
- Hauser, M.D. (1993). Right hemisphere dominance for the production of facial expression in monkeys. *Science*, 261, 475-477.
- Hook-Costigan, M.A. (1999) Eye preferences of marmosets for viewing novel stimuli and their relationship to hand, foot and facial expression asymmetries. *International Journal of Comparative Psychology*, 11.
- Hook-Costigan, M.A. & Rogers, L.J. (1995). Hand, mouth and eye preferences in the common marmoset (*Callithrix jacchus*). *Folia Primatologica*, 64, 180-191.
- Hook-Costigan, M.A. & Rogers, L.J. (1997). Hand preferences in New World primates. *International Journal of Comparative Psychology*, 9, 173-207.
- Hook-Costigan, M.A. & Rogers, L.J. (1998a). Lateralized use of the mouth in production of vocalisations by marmosets. *Neuropsychologia*, 36, 1265-1273.
- Hook-Costigan, M.A. & Rogers, L.J. (1998b). Eye preference in common marmosets (*Callithrix jacchus*): Influence of age stimulus and hand preference. *Laterality*, 3, 109-130.

- Hopkins, W.D. & Bennett, A. (1994). Handedness and approach-avoidance behaviour in chimpanzees. *Journal of Experimental Psychology*, 20, 413-418.
- Kaplan, G. & Rogers, L.J. (1999a) Parental care and exploration in the common marmoset. *International Journal of Comparative Psychology*, 12, 21-34.
- Kaplan, G. & Rogers, L.J. (1999b) Parental care in the common marmoset: Anogenital licking and effect on exploration. *Journal of Comparative Psychology*, in press.
- Kappeler, P.M. (1987) The acquisition process of a novel behavior pattern in a group of ring-tailed lemurs (*Lemur catta*). *Primates*, 28, 225-228.
- King, J.E. (1995). Laterality in hand preferences and reaching accuracy of cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, 109, 34- 41.
- Menzel, C.R. (1980) Head cocking and visual perception in primates. *Animal Behaviour*, 28, 151-159.
- Menzel, E.R. & Menzel, C.R. (1979). Cognitive, development and social aspects of responsiveness to novel objects in a family group of marmosets (*Saguinus fuscicollis*). *Behaviour*, 70, 251-279.
- Rogers, L.J., Stafford, D. & Ward, J.P. (1993). Head cocking in galagos. *Animal Behaviour*, 45, 943-952.
- Rothe, H. & Koenig, A (1991). Variability of social organisation in captive common marmosets (*Callithrix jacchus*). *Folia Primatologica*, 57, 28-33.
- Tardif, S.D., Harrison, M.L. & Simek, M.A. (1993) Communal infant care in marmosets and tamarins: Relation to energetics, ecology, and social organisation. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, Behavior, and Ecology* (pp. 220-234), Oxford, England: Oxford University Press.
- Ward, J.P., Milliken, G.W., Dodson, D.L., Stafford, D.K. & Wallace, M. (1990). Handedness as a function of sex and age in a large population of lemur. *Journal of Comparative Psychology*, 104, 167-173.
- Watson, S.L. & Ward, J.P. (1996). Temperament and problem solving in the small-eared bushbaby (*Otolemur garnettii*). *Journal of Comparative Psychology*, 110, 377-385.
- Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, 9, 442-446.

Instructions to Authors

All manuscripts are reviewed by two readers other than the Editors. Authors should send three copies of their manuscripts to one of the Editors. One diskette copy saved in ASCII format or as a standard word processor file, will need to be submitted to the Editor once the manuscript is accepted for publication. Electronic versions of figures are also preferred at this stage. Indicate clearly on the diskette the author(s) name(s), file format and program version number. (Alternate arrangements may be possible for those authors who are unable to provide a diskette copy).

The manuscript should have a cover page with the full title, the author(s) name(s) and address(es) and should indicate the person with whom the Journal may correspond. If the author(s) has(ve) an electronic mail address or fax number, these should be given in a cover letter accompanying the manuscript. The abstract should be on a separate page. All articles are published in English; the author(s) should also submit an abstract in their language if it does not require non-Roman type. Author(s) are responsible for the accuracy of the non-English abstract. Acknowledgements should appear on a separate page and carry the title of the article and the author(s) name(s). If the author(s) prefer(s) anonymity in the review process, this should be stated in a covering letter and the manuscript, abstracts, and illustrative material should carry only the title of the article. The cover sheet and acknowledgements will not be sent to the reviewers in this instance.

GENERAL REQUIREMENTS Logical organization is essential. While headings help to structure the content, titles and headings within the manuscript should be as short as possible. Tables and figures should not be redundant. Illustrative material should be self-explanatory and used sparingly. Tables and figures must be in camera-ready condition and include separate captions. Labels on figures should be either Helvetica or Times Roman font and be sufficiently large to allow clarity when reduced. Black and white shading is preferred to more complex fill patterns. Electronic versions of all figures should be included on the final submitted diskette if possible. Only items cited in manuscripts should be listed as references. Page numbers must be provided for direct quotations. Footnotes should not be used except in special circumstances and with permission of the Editor.

MANUSCRIPTS should be double-spaced, the original on white bond paper, with margins of 3 cm on all four edges and approximately 26 lines to the page. Manuscripts longer than 20 typed pages (not counting figures, tables, and references) will only be considered in unusual circumstances. The current style manual of the American Psychological Association is to be followed. Manuscripts which do not meet the style requirements will be returned for retyping.

REFERENCES should be listed on a separate page and referred to in the text by author(s) and year of publication as in the Publication Manual of the American Psychological Association.



International Society for Comparative Psychology